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THE REPRODUCTIVE ANATOMY AND CHROMOSOME NUMBER OF *QUICKIA SPURCA* (GOULD) (STYLOMMATOPHORA: HETERURETHRA: SUCCINEIDAE)[1]

C. M. Patterson

The succineid genus *Quickia* was named by Odhner (1950) in honor of H. E. Quick, who was the first to describe the unique anatomical features of *Q. concisa*. Odhner placed *Quickia* in the subfamily Catinellinae and pointed out its apparent relationship to *Indosuccinea* (both have the tentacular retractor muscle passing on the inner side of an exceptionally small penis). He further described *Quickia* as characterized by "...penis retractor crossing outside of vagina. Radula narrow, laterals and marginals equal in number (about 10 of each), the latter broad; entocones both in laterals and marginals. Shell small, with microgranular sculpture... (type *S. concisa* Morelet 1848)." After studying the above 2 genera, Odhner stated that "*Quickia* and *Indosuccinea* evidently both represent a more primitive stage of the male genital development than exists in the other species of the Catinellinae and indeed the most archaic type of male organ in any of the Succineidae hitherto examined."

During the past few years there have been several papers published on chromosome numbers in the Succineidae (see Literature Cited, p 12-13). Previously, the known haploid chromosome numbers in the Succineidae corresponded rather well to subfamily groupings based on internal reproductive anatomy. Haploid chromosome numbers reported for 6 members of the more primitive subfamily Catinellinae (comprising those species that lack a penial sheath) were n=5 or 6[2]; whereas in the Succineinae (comprising species possessing a penial sheath) the haploid chromosome numbers range from n=11-22 among the 27 species studied (Patterson, 1968). Thus, from past studies, there seemed to be some correlation between "primitiveness" in an anatomical sense and low chromosome numbers.

With this in mind, I was anxious to determine the chromosome number in a genus considered to be anatomically more primitive than all other succineid genera yet studied cytologically. This paper is concerned with the chromosome number and aspects of reproductive anatomy of *Quickia spurca* from Liberia.

MATERIALS AND METHODS

Most of the snails used in this study are laboratory reared descendants of specimens collected by Dr. William Sodeman from a population situated in a damp area of ground immediately around and upon the moist sides of brick foundation pillars of a residence at the Liberian Institute for Tropical Medicine, Harbel, Liberia. Two shipments of specimens were received, one on October 2, 1968 and the other November 11, 1968.

Snails used for anatomical studies were relaxed in tap water to which a few

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[2]These are the lowest chromosome numbers reported in the Mollusca.

menthol crystals had been added. When the animals were fully extended and gave no reaction to tactile stimulation (usually after 14-16 hours), they were killed and fixed in a solution of alcohol-formalin-acetic acid (Lavdowsky's mixture). After 15 minutes the snails were rinsed and preserved in 70% ethanol to which 1% (by volume) glycerin had been added to keep the animal parts soft and some color preserved. The dissections were made in this ethanol-glycerin preservative. Dissections were made using fine watchmaker's forceps and iridectomy scissors in a petri dish half filled with solidified paraffin, blackened with activated charcoal. Tips of #00 stainless steel insect pins were used when needed to hold the soft parts in position. A Wild M5 stereoscopic microscope equipped with a camera lucida was used to make dissections and drawings of shell and anatomy.

Animals were fixed in Newcomer's (1953) fluid for cytological studies. Ovotestes were dissected from the fixed animals, and chromosome preparations of these were made using the acetic-orein squash technique (La Cour, 1941). Chromosomes were observed using a Leitz compound microscope with 10X oculars and 90X (n.a. 1.32) light field and 100X (n.a. 1.30) phase contrast oil immersion objectives. The chromosome drawing (Fig. 11a) was made using a camera lucida attachment and reproduced at a table-top magnification of 6800X. Photographs were taken using oil immersion objectives, Nikon Microflex model EFM semi-automatic photomicrographic attachment, Nikon film holder and Kodak high contrast copy film.

IDENTIFICATION OF MATERIAL

Identification of species of the Succineidae using shell characters is often extremely difficult or impossible. In fact, some species cannot even be assigned confidently to a genus using such characters. However, due to the unavailability of comparative anatomical material, I have resorted to basing the identification of my material partially on shell morphology, but not without reservations.

I was first inclined to identify my specimens as *Quickia concisa* (Morelet), a species reported to occur in Liberia (Odhner, 1950). However, some differences in anatomy of the reproductive tract caused doubt that my specimens were *Q. concisa* (see Table 1). Furthermore, Quick (1936) and Dr. C. A. Wright (personal communication) have in every case found the shell of *Q. concisa* to be encrusted with mud arranged in 3 spiral rows. Quick (1936) states that "the mud is firmly adherent, and attempts to remove it, even after long soaking, bring away the periostracum with it, leaving the shell silvery white." Presumably he was referring to shells of dead animals on which the mud had dried. Photographs of syntype specimens of *Q. concisa* (Wright, 1963, pl. 14) show the shells to be devoid of any spiral rows of mud and Wright (personal communication) thinks that these specimens had been treated and had lost their periostracum. Most of the field collected specimens I received were encrusted with mud and several showed a definite spiral arrangement of mud rows. However, in most specimens there did not appear to be such a special arrangement of the mud and within a day after the specimens were placed in laboratory culture containers little mud remained on any of the larger specimens. Young specimens (2-3 mm) raised in the laboratory often show 3 spirally arranged rows of mud on the body whorl, but this condition is never maintained to maturity. The shells of other specimens are simply encrusted with mud in varying amounts, which is not arranged in any special pattern, while others are almost free of any mud. Twelve young individuals exhibiting mud rows were isolated and allowed to mature. They were not anatomically distinct from forms that never possessed the mud rows. It should be mentioned that on

Q. concisa specimens from Mauritius, which were identified for Madge by Quick, encrusted mud was not always deposited in spiral rows but in a reticulate pattern in some individuals (Madge, 1938). Therefore, the presence of the spiral arrangement of mud is not a reliable species character for identifying *Q. concisa*. Additionally, the nature of the habitat, especially substrate and cover, can perhaps produce variability in shell-mud characteristics. Also, inasmuch as encrustation of mud on the shell is common with many succineid species, it would not be surprising to find 2 closely related species of *Quickia* exhibiting the same spiral pattern of mud rows.

There was some variation in shell shape of both the field-collected (Fig. 2) and laboratory-reared specimens used in this study. Fig. 1 shows camera lucida drawings of 4 individuals, each having a somewhat different shell shape. The shell illustrated in Fig. 3 was most typical. In comparing my specimens with the type lot of *"Succinea" spurca* Gould (cat. no. 169378, Museum of Comparative Zoology, Harvard University) I found striking similarities. All of the paratype specimens were encrusted with some mud, and on the body whorl of 4 of the 18 specimens there appeared to be a spiral arrangement of 3 mud rows; 4 rows were present on another individual. The amount of mud varied on the remaining 13 specimens, and was not arranged in any special manner; 5 of these latter specimens had only a meager amount of mud on the shell.[3] The mud had been cleaned from the lectotype of *"S." spurca* (cat. no. 169377, Museum of Comparative Zoology) shown in Fig. 4b. Specimens of the type lot of *"S." spurca* were collected from "...moist sides of water-pits, and in crevices of trees" (Gould, 1850). Such habitats are likely to be very similar in humidity and substrate to that at the Liberian Institute for Tropical Medicine where my specimens were collected. The type lot of *"S." spurca* shows a variability in shell shape similar to that exhibited by my specimens.

Pilsbry (1919) in reference to *"S." concisa* stated: "This species is probably, as Ancey [1888] has stated, identical with *S. spurca* Gould, described from Liberia." Ancey's opinion was based on the shell. Due to differences in anatomy (when compared to Quick's description), it does not seem likely that my specimens are *Q. concisa*. But, on the other hand, shells of my specimens cannot be distinguished from the type specimens of *"Succinea" spurca* Gould, hence this name will be used. Should it be discovered that *Q. spurca* is indeed synonymous with *Q. concisa*, then these specimens represent a new species.

REPRODUCTIVE ANATOMY

The anatomy of the reproductive system has been described by Quick (1936) for *Quickia concisa*. Anatomically, *Q. spurca* is certainly closely related to *Q. concisa*.

The shell of *Quickia spurca* is from 6.5 mm to 8.5 mm length in specimens having 2 1/2 to 3 whorls and is a pale straw color. Like *Q. concisa*, the shell possesses a sculpture of fine striae in the line of growth, and when the periostracum is removed, the shell has a silvery-white appearance. Encrustation of mud on the shell was discussed previously above. Mature specimens of *Q. spurca* usually do not possess the prominent spiral mud lines which Quick (1936) points

[3]Gould (1850) states that *"S." spurca* is "Similar to *S. avara* [=*Catinella vermeta*] in form and in the peculiarity of becoming invested with an earthy coating." He does not mention spiral mud rows and *C. vermeta* does not show such a spiral arrangement of mud, but simply becomes encrusted with mud.

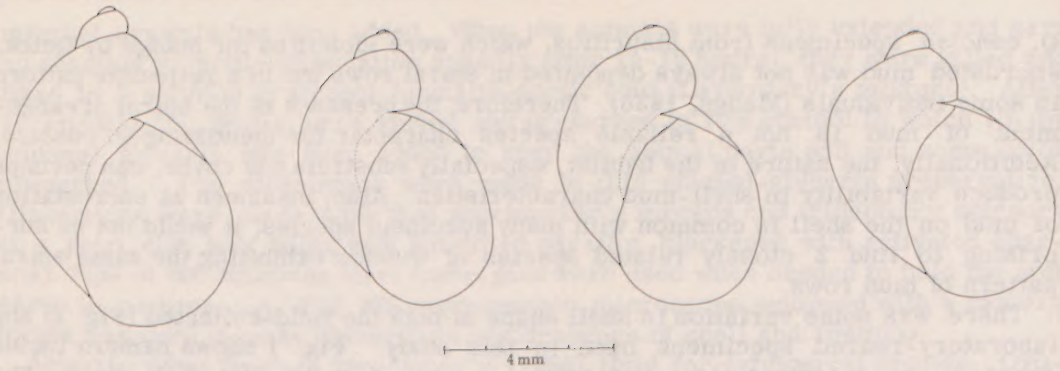

FIG. 1. Shell shapes of 4 laboratory reared adult *Quickia spurca*.

out to be "very characteristic" for *Q. concisa*.

The body of the living animal is rather translucent and appears to be almost colorless except for that color showing through from the internal organs and sparse pigmentation on the mantle in some individuals. The kidney has the shape outlined in Fig. 5 and is pale yellow in color. The digestive gland is a soft brown. The black pigment spots on the tentacle retractor muscles (Fig. 9a, b, c) are readily visible through the body wall. Mantle pigmentation varies from almost none to the maximum amount shown in Fig. 5. Additionally, on all specimens there is a sparse amount of pigmentation on the sides of the body wall immediately behind the base of the tentacles (Fig. 5). *Quickia spurca* differs from *Q. concisa* in that the former lacks pigmentation near the respiratory opening. The foot of mature, relaxed and fixed animals averages 11-12 mm in length and 5-6 mm in width, thereby being about twice the size of the specimens studied by Quick.

A detailed study of the radula and jaw was not undertaken. However, they do not seem to differ significantly from the condition described for *Q. concisa*. Odhner (1950), relying partly on Quick's work, characterized the genus *Quickia* as having lateral and marginal teeth equal in number. Inspection of the radula of 3 individuals of *Q. spurca* show 11 laterals and 12 marginals. However, the relative number of

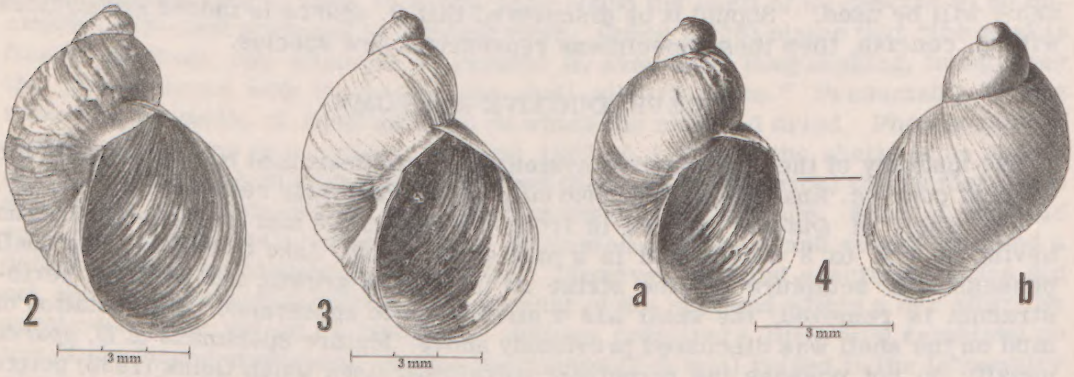

FIG. 2. Shell of adult *Quickia spurca* specimen received from the field.

FIG. 3. Typical shell of laboratory reared adult specimen of *Quickia spurca*.

FIG. 4. (a) Apertural view of lectotype of *Quickia spurca* Gould; (b) Back view of lectotype.

lateral and marginal radular teeth is often a variable character within the Succineidae (Quick, 1936) and cannot be used with assurity as a generic characteristic.

A ventral view of the reproductive tract of *Quickia spurca* is shown in Fig. 6. The ovotestis, consisting of 50-60 acini, is rather small, dull beige to cream in color, and in some cases, sparsely pigmented with black. The hermaphroditic duct is nearly straight, somewhat dilated in the middle and without pigmentation. Two small, white seminal vesicles of unequal size join to form a common duct with the hermaphroditic duct. A short distance beyond these, and just distal to the spermoviduct, the albumen gland duct joins the hermaphroditic duct, and their common channel opens immediately into the distal portion of the spermoviduct. The albumen gland is large, follicular and linguiform in shape. The spermoviduct is folded tightly along its length. The prostate gland is unique in the 3 species of *Quickia*[4] I have examined, differing considerably from the condition I have observed in the genera *Succinea*, *Oxyloma*, *Catinella* and *Omalonyx*. The prostate gland of *Q. spurca* appears as a rather loose collection of oblong-spheroid-shaped bodies that are a bright, opaque white in color (Fig. 6).[5] On dissection, these bodies are found to be 5 to 7 bunches of branching tubules (Fig. 7). A varying number of tubules join together at a common collecting duct which empties into the vas deferens. Quick made no mention of this unique character in *Q. concisa*, and described its prostate to be yellow and very small (Quick, 1936). The oviduct of *Q. spurca* is somewhat more loosely folded than the spermoviduct. The folds in the oviduct are noticeable from its outside as it approaches the point of entry of the spermathecal duct (at the apex of a rather long S-bend between the vagina and oviduct). The vagina is long and twisted 180° between its distal and proximal portions. Inner folds are externally visible along most of the length of the vagina, except for its terminal 1/4, where the wall becomes highly muscular. The spermatheca is nearly spherical with its duct departing from its dorsal-distal surface. The spermathecal duct is slightly more than 3 times the length of the penis[6]. The vas deferens courses ventrally from the prostate and passes dorsally over the vagina, wrapping around to the ventral side of the vagina, and inserts at the apex of the penis in close proximity to the penial retractor muscle.

The penis is a small simple tube about 1 mm in length (Fig. 8a), containing prominent inner folds especially noticeable in cross-section (Fig. 8b). These folds are not visible through the wall of the penis when viewed from the outer surface. The delicate penial retractor muscle is rather thin and very long. The penial retractor muscle without exception courses forward beneath the anterior intestinal loop and kidney and terminates dorsal to the albumen gland. Quick (1936) describes the penial retractor in *Q. concisa* as "short and slender... arises much more anteriorly from the body-wall on the right side of the neck, near the front end of the diaphragm." This condition has never been observed in *Q. spurca*. Odhner (1950) verified Quick's results and regarded lack of differentiation and enclosure of the penial retractor in the integumental musculature as a primitive stage. However, from the current study, it is obvious that the penial retractor arrange-

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[4] *Quickia spurca*, *Q.* sp. from Aldabra atoll and *Q. gravelyi* from India.

[5] The prostate gland of *Q.* sp. (Aldabra) is similar to *Q. spurca* while that of *Q. gravelyi* is more compact and pale creamy yellow in color.

[6] Odhner (1950) characterizes *Quickia* as having a penis 1/3-1/4 the length of the spermathecal duct.

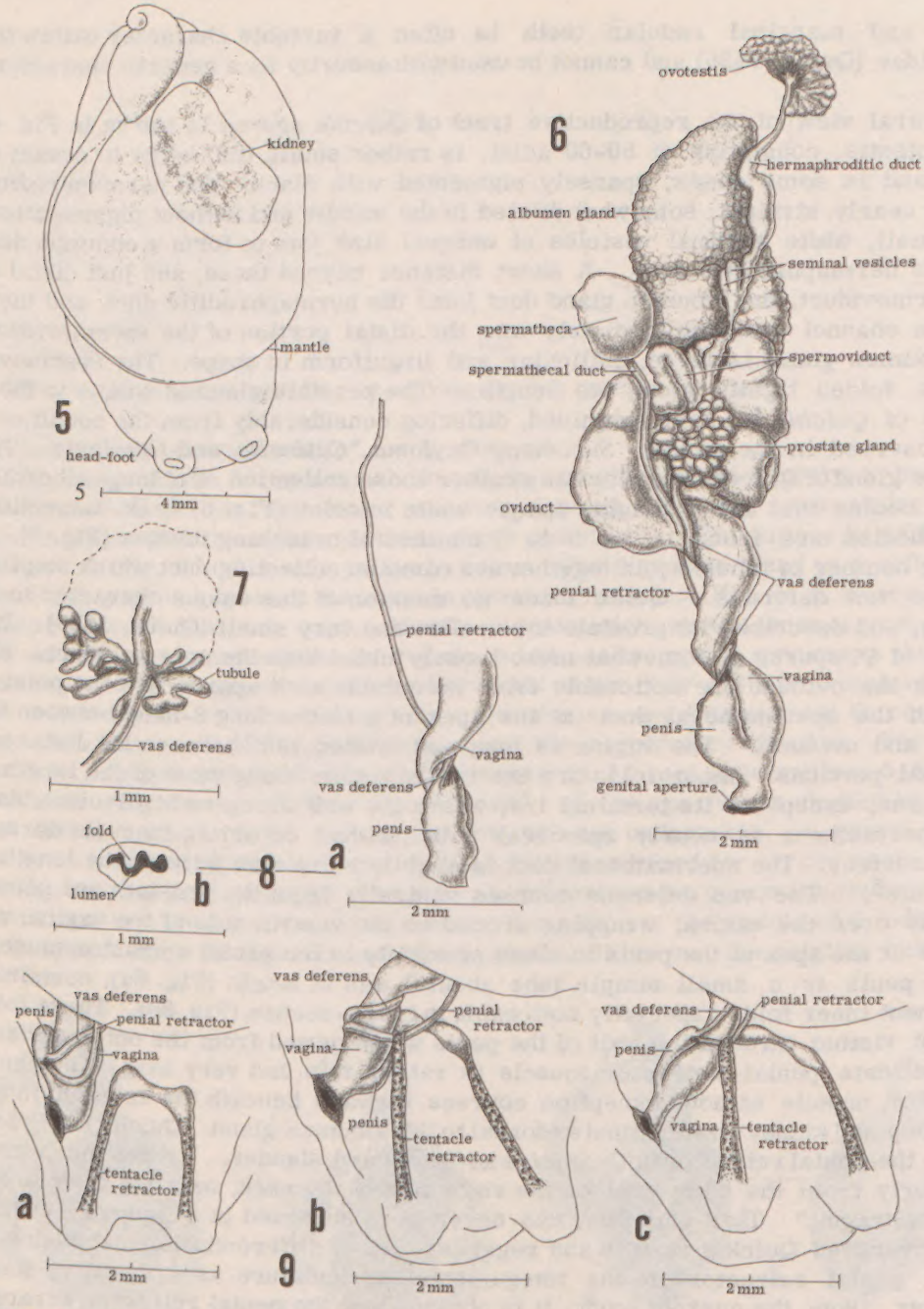

FIG. 5. Pigmentation pattern in *Quickia spurca*.

FIG. 6. Ventral view of the reproductive tract.

FIG. 7. Dorsal view of the prostate gland.

FIG. 8. (a) Penial complex, right side view; (b) Cross-section of the penis.

FIG. 9a, b, c. Variation in the relationship of the penial and tentacular retractor muscles and orientation of the terminal genitalia in 3 specimens of *Quickia spurca*.

FIG. 10. (a) Diagrammatic representation of a portion of the ancient Gondwanaland continent (modified from Hurley, 1968); (b) Known distribution of *Quickia*. 1, Sierra Leone; 2, Liberia; 3, Cameroon; 4, Gabon; 5, Sãn Thomé; 6, Angola; 7, Zanzibar; 8, Seychelles; 9, Aldabra; 10, La Réunion; 11, Mauritius; 12, Rodriguez; 13, Madras State; 14, Madras State.

TABLE 1. Comparison of morphological features of *Quickia spurca* and *Q. concisa*

Character	Comparison of characters	
	Similar	Different
Shell shape	X	
Shell sculpture	X	
Mud encrustation		X
. . .		
Pigmentation on body		X
. . .		
Ovotestis		X
Hermaphroditic duct	X	
Seminal vesicles	X	
Albumen gland	X	
Prostate gland		X
Spermatheca and duct	X	
Spermoviduct and oviduct	X	
Vagina	X	
Penis	X	
Penial retractor muscle		X

TABLE 2. Haploid chromosome numbers in the Catinellinae

Species	Haploid No.	Source	Reference
Catinella			
C. (*Catinella*) *rotundata*	5	Oahu I., Hawaii	Burch, 1964a
C. (*C.*) *putamen*	5	W. Samoa	Patterson (unpublished)*
C. (*Mediappendix*) *vermeta*	6	U.S.A.	Burch, 1964b
C. (*M.*) *texana*	6	U.S.A.	Natarajan, Hubricht & Burch, 1966
C. (*M.*) *aprica*	6	U.S.A.	Patterson (unpublished)*
C. (*M.*) cf. *gabbi*	6	U.S.A.	Burch, Patterson & Natarajan, 1966
C. (*M.*) sp.	6	Mexico	Patterson (unpublished)
C. (*Quickella*) *arenaria*	6	England	Butot & Kiauta, 1967
Quickia			
Q. spurca	25	Liberia	Patterson (this paper)*
Q. gravelyi	25	South India	Patterson (unpublished)*
Q. sp.	25	Aldabra	Patterson (unpublished)*

*Listed in Patterson (1969)

ment in *Q. concisa* is not common to all species of *Quickia*. There is a great amount of variation in the relative orientation of the penis and vagina as shown in Fig. 9 a, b, c. The right tentacle retractor muscle always passes on the inner side of the terminal reproductive tract complex. The penial retractor muscle may either pass underneath (Fig. 9 b, c) or over (Fig. 9a) the right tentacular retractor muscle. Each condition is encountered with about equal frequency. There is also variability in the length of the common terminal reproductive tract. It is most commonly rather long (Figs. 6, 9c), but was short in a few specimens (Fig. 9a) and intermediate in length in a few others (Fig. 9b). Comparisons of some morphological features of *Q. spurca* and *Q. concisa* are shown in Table 1.

CHROMOSOME NUMBER

The haploid chromosome number of *Quickia spurca* is n=25, the same number observed in *Q. gravelyi* from South India and an unidentified species from Aldabra atoll (listed in Patterson, 1969). These are the highest chromosome numbers yet reported in the Succineidae. The conservativeness with regard to chromosomal number change in the Gastropoda has been discussed elsewhere (Burch, 1965; Patterson, 1969). This same conservativeness appears at the generic or subgeneric group level in the Succineidae, but as a group, this family is quite diverse, with haploid chromosome numbers ranging from 5 to 25. This wide range of chromosome numbers belongs specifically to the subfamily Catinellinae (Table 2); chromosome numbers of other Succineidae range from 11 to 22.

Geographical distribution and cytological data of members of the Catinellinae is worth noting. Two species of *Catinella* inhabiting Pacific islands (subgenus *Catinella* s.s.) have 5 pairs of chromosomes. The North American-European *Catinella* complex is characterized by having 6 pairs of chromosomes. The Afro-Indian *Quickia* species have 25 pairs of chromosomes. The theory of continental

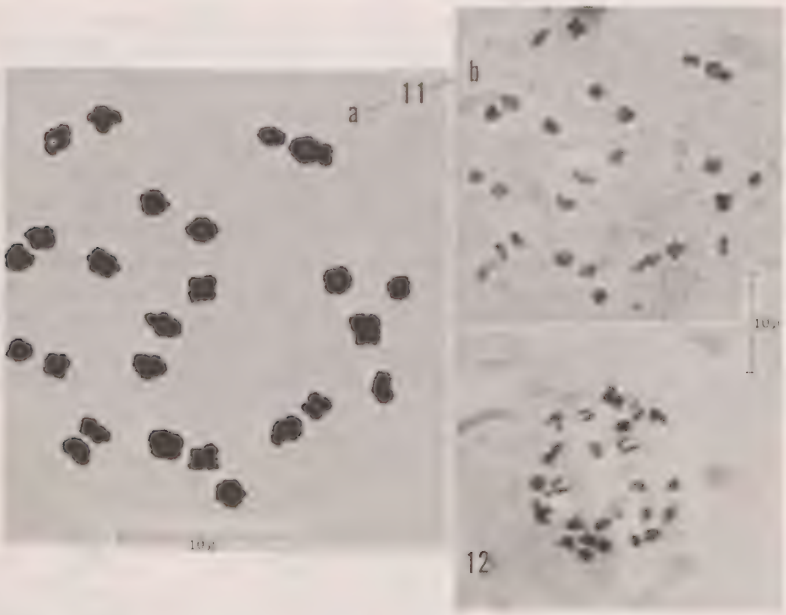

FIG. 11. (a) Meiotic Metaphase I chromosomes of *Quickia spurca* (camera lucida drawing 6800X); (b) Photograph of the above cell.

FIG. 12. Photograph of meiotic diakinesis chromosomes of *Quickia spurca*.

drift (Wegener, 1966) which recently has gained considerable substantiation (e.g., see Darlington, 1965; Hurley, 1968; Kurtén, 1969), holds that the African continent and India, as recently as 200 million years ago, were once joined as part of a huge continent, Gondwanaland (Fig. 10a). If this were indeed true, it does not seem unreasonable to find closely related species of *Quickia* in the geographical regions of West Africa, Aldabra (off the east coast of Africa) and South India. Based on the limited information available, the known distribution of *Quickia* is shown in Fig. 10b. Odhner (1950) states in regard to the distribution of *Quickia*, "This peculiar distribution [excluding India] seems to indicate a splitting up of a once continuous circum-African range perhaps combined with the old Gondwana continent." These observations, of course, do not negate the possibility that the species of *Quickia* were distributed by factors other than a geological event or series of events occurring in the past. In any case, based on the limited amount of cytological data now available for members of the Catinellinae, there appears to be a geographical-cytological correlation. It will be most interesting to observe whether future studies bear out this apparent relationship.

It is unfortunate that there were no mitotic cells suitable for karyotype analysis. In the few mitotic cells present, 2 pairs of conspicuously large chromosomes were observed. The meiotic diakinesis bivalents appear in most cells as ring or cross-shaped figures of varying sizes. Occasionally a rod-shaped bivalent is observed in diakinesis. Fig. 12 shows a photograph of a cell in diakinesis. The highly condensed chromosomes of meiotic Metaphase I are drawn in Fig. 11a, and a photograph of this cell is shown in Fig. 11b. Most of the morphological features of the diakinetic chromosomes are obscured by their highly condensed state in Metaphase I.

A thorough comparative cytological study based on karyotype analyses of African and Indian species of *Quickia* is desirable. Since *Indosuccinea* is anatomically related to *Quickia*, it is also important to compare members of this genus to *Quickia*.

Information on haploid chromosome numbers of succineid snails compiled previous to the current study suggested a good correlation between chromosome numbers and subfamily groupings based on anatomy (Patterson, 1968). Members of the morphologically more primitive subfamily Catinellinae had 5 or 6 pairs of chromosomes, while species of the subfamily Succineinae all had more than 11 pairs of chromosomes and usually 17-18 pairs. It was noted, however, that cytological information was incomplete for the family, and that such a correlation may not be borne out by further studies (Patterson, 1968, 1969). The recent finding that *Quickia* has 25 pairs of chromosomes sheds doubt on the apparent correlation that was thought to exist. We are now left with 2 considerations: (1) Such a correlation between chromosome number and subfamily groupings does not exist, or at least is incomplete, or (2) a re-evaulation of the relationships among succineids may necessitate a change in the current taxonomy of the family. Perhaps 3 or more major groupings (subfamilies?) exist in the Recent Succineidae.

DISCUSSION

Quickia is a most interesting succineid genus which has received little attention. Several questions have now arisen from this brief study: (1) Will future studies bear out a geographical-cytological relationship on a world-wide basis in the Catinellinae? (2) Does there indeed exist a true Afro-Indian geographical-cytological relationship which has some historical correlation to continental drift? (3) What are the limits of variation at the generic level in *Quickia*? and

(4) What is the systematic relationship of *Quickia* to other succineid genera, especially to *Catinella* and *Indosuccinea*?

Clearly, many more species of Catinellinae need to be studied to ascertain the suggestion that there may exist a geographical-cytological relationship. If there is a correlation between the distribution of *Quickia* and the existence of Gondwanaland, then areas of South America which were apposed to the present Liberian and Gulf coast of West Africa, and the western coast of Australia which was apposed to South India, need to be surveyed to determine if anatomically and cytologically related species occur on these continents.

Odhner (1950) based his generic description on specimens of the only species available to him, *Quickia concisa*. Comparison of an additional species, *Q. spurca*, has shown great variation in the penial retractor muscle insertion, as well as differences in other morphological features. Thus, many more species need to be studied anatomically in order to define the morphological parameters of this genus.

The question of the systematic relationship of *Quickia* to other members of the subfamily Catinellinae needs to be answered. *Quickia* and *Indosuccinea* seem to be clearly related on anatomical grounds, and together they form a grouping very distinct from *Catinella*. Whether or not *Lithotis* and *Camptonyx* are related to *Quickia* and *Indosuccinea* needs to be determined. Rao (1925) recognized some similarities between *Lithotis* and *Indosuccinea*, but considered *Lithotis* to be unique among the Succineidae. Information on the chromosome number of this genus would aid in the clarification of its systematic relations to other Succineidae, especially to *Indosuccinea* and *Quickia*. Assuming absence of polyploidy, *Quickia* is undoubtedly quite distinct cytologically from *Catinella*, and a more thorough anatomical and a cytological study of *Quickia* and its allies may necessitate the creation of a separate subfamily (Quickinae).

ABSTRACT

Quickia is a primitive succineid genus belonging to the subfamily Catinellinae. The morphology of only 1 species, *Q. concisa*, has been reported previously. This paper describes the reproductive anatomy and chromosome number of *Q. spurca* (Gould) from Liberia.

Generally, the morphological features of *Quickia spurca* agree with those described by Quick (1936) for *Q. concisa*. However, there are several points of difference, especially in regard to the reproductive anatomy. The most obvious difference between these 2 species is in the length and insertion of the penial retractor muscle.

The haploid chromosome numbers previously reported in the Catinellinae are n=5 and n=6 for *Catinella*. The present study shows that *Quickia* has 25 pairs of chromosomes. This may indicate that *Quickia* and *Catinella* are not as closely related as currently believed. Within the Catinellinae, there appears to be a geographical-cytological correlation based on chromosome number. The distribution of *Quickia* may have some historical connection to the existence of Gondwanaland.

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ERINNA NEWCOMBI OF HAWAII AND *LIMNAEA ONYCHIA* OF JAPAN[1]

J. B. Burch

Shells of the freshwater pulmonate snail family Lymnaeidae (Basommatophora: Branchiopulmonata) are generally high-spired, a condition which is especially exemplified by most species of the nominal groups *Lymnaea* s.s., *Stagnicola*, *Acella*, *Bulimnea* and *Fossaria* (Fig. 1). Species of the *Pseudosuccinea* and *Radix* groups tend to have relatively smaller spires (Fig. 2), with correspondingly larger terminal whorls ("body whorls"), and some species of the latter group (e.g., *R. auricularia*), as well as related groups (*Myxas*, *Bullastra*) and some species of *Austropeplea*, have even smaller spires relative to their especially large body whorls (Fig. 3). Two species of the lymnaeid subfamily Lymnaeinae are noteworthy because the extreme reduction of their spires gives them a "neritiform" appearance (Fig. 4),[2] a term derived from the shape of many species of the prosobranch family Neritidae (Archaeogastropoda: Neritacea) (Fig. 5). Coupled with this neritiform shape in these lymnaeids is a very small shell size. These 2 species are *Erinna newcombi* H. & A. Adams 1855 of Kauai Island, Hawaii, and *Limnaea onychia* Westerlund 1883, of Lake Biwa, Japan.

The original descriptions of these 2 neritiform lymnaeid species are as follows:

Erinna newcombi [H. & A. Adams, 1855, p 120], Fig. 6.

> *E. testa olivacea tenui longitudinaliter oblique striata, spira brevissima, obtusa, apice erosula, anfractu ultimo ventricoso; apertura semiovata; columella recta excavata, labro tenui.*
>
> *Hab.* Heneta River, Kami, Sandwich Islands. (*Dr. Newcomb.*)
>
> This shell by some would be referred to *Neritina*, by others to *Limnaea*, and possibly by a few to the genus *Otina*; it appears, however, to be distinct in character from all these.[3]

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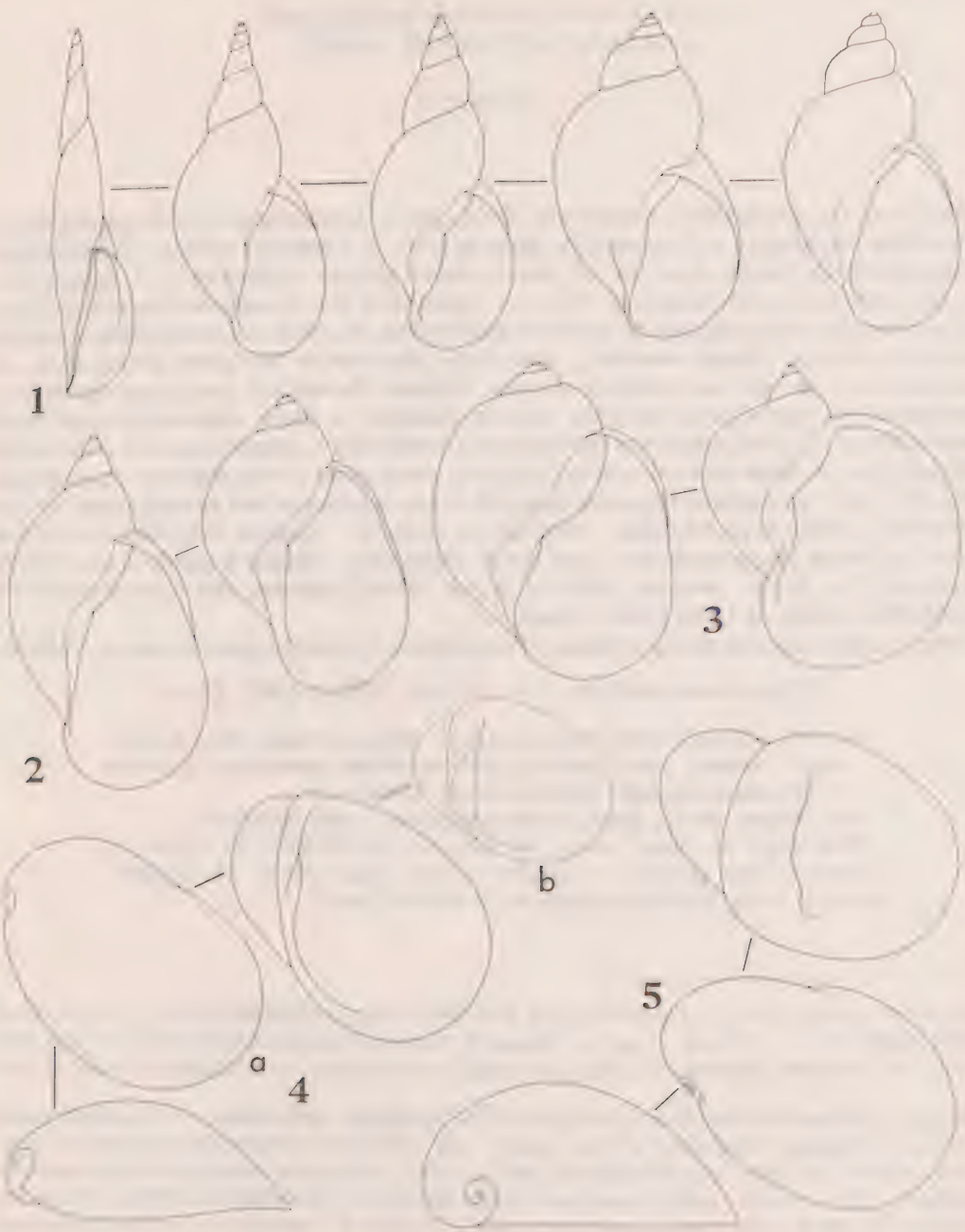
[1]Supported (in part) by a research grant (GB-5601) from the National Science Foundation, Washington, D. C., U.S.A., and a Research Career Program Award (5-K3-AI-19, 451) from the National Institute of Allergy & Infectious Diseases, U.S. Public Health Service.

[2]Nearly all lymnaeid species are assigned to the subfamily Lymnaeinae, but a small group of limpet-shaped lymnaeids of the genus *Lanx*, found in western North America, have been placed in their own subfamily, the Lancinae (sometimes considered as a separate family). This latter group comprises forms that have proceeded even further in the direction of shell reduction, producing a shell in which all remnants of coiling have been lost.

[3]The figure of *Erinna newcombi* (Fig. 6a) published by H. & A. Adams (1858) looks more like *L. aulacospira* Ancey, but their reference to *Neritina* and *Otina* in the original description would seem to refer it to our current understanding of *E. newcombi*, as does Hubendick's (1952) figure of the "type of *Errinna newcombi* [Brit. Mus. 1950-5-19. 13-14]." I have not yet determined the source of Thiele's figure (fig. 572, p 477) of "*Erinna newcombi* H. & A. Adams vergr." (Fig. 6b).



FIGS. 1-5. Lymnaeid shells and *Neritina*. [Scales in mm]

FIG. 1. High-spired lymnaeid shells. a, *Acella* (N. Amer.); b, *Lymnaea* (Holarctic); c, *Stagnicola* (Holarctic); d, *Bulimnea* (N. Amer.); e, *Fossaria* (= *Galba*) (Holarctic; African).

FIG. 2. Spired lymnaeid shells with relatively large body whorls. a, *Pseudosuccinea* (N. Amer.); b, *Radix* [Taiwan] (Eurasian, African).

FIG. 3. Lymnaeid shells with especially large body whorls. a, *Austropeplea* (Australasian); *Radix* [U. S. A., introduced from Europe] (Eurasian, African).

FIG. 4. Neritiform lymnaeids. a, *Limnaea onychia* (Japan); b, *Erinna newcombi* (Hawaii).

FIG. 5. *Neritina* (Neritidae), exhibiting a typical "neritiform" shell.

Limnaea onychia [Westerlund, 1883, p 52], Fig. 7c.

Testa rimata, ovata, rufescenti-cornea, tenuis, dense regulariter striata, extus vix nitidula, intus nitida; spira brevissima, lateralis, saepissime erosa; anfr. 2 1/2, ultimus testam fere totam efficiens, penultimus subtus tumidus, ult. convexus; apert. maxima, late elliptico-ovata, basi circularis, superne in auriculo libero acutiusculo producta, marginibus plica columellari subconjunctis, columella arcuata, parum contorta. Dimens. spec. max.: Long. 6 1/2, diam. obliq. 5, transvers. 4 mm; ap. 5 mm longa, 4 mm lata.
Japan, ad litora lacus Biva.

Limnaea onychia was later described by Preston (1916) as *Lithotis japonica*, sp. n., a clear synonym of the above, but he placed it in the land snail family Succineidae, and referred it to a genus restricted to India. This placement was corrected by Annandale & Prashad (1919). Preston's original description is as follows:

Lithotis japonica [Preston, 1916, p 160], Fig. 7a.

Shell imperforate, small, ovate, reddish brown; whorls 2 1/2, the first small, the last very large, transversely striate and slightly angled above, laterally compressed; columella margin obliquely descending, flattened, broad; labrum continuous, acute; aperture large, slightly dilated.

Alt. 1.5, diam. maj. 4, diam. min. 3 mm.

Aperture: alt. 2.5, diam. 2 mm.

Hab. Lake Biwa, Japan; on the lower surface of stones at the edge of the lake (*Dr. N. Annandale*).

The shell in general form recalls, in miniature, the genus *Septaria*.

For both of the 2 above species, a separate genus has been erected, *Erinna* by H. & A. Adams for *E. newcombi*, and *Omia* by Annandale & Prashad for *Lithotis japonica* Preston [=*Limnaea onychia* Westerlund].[4] The original generic diagnoses are as follows:

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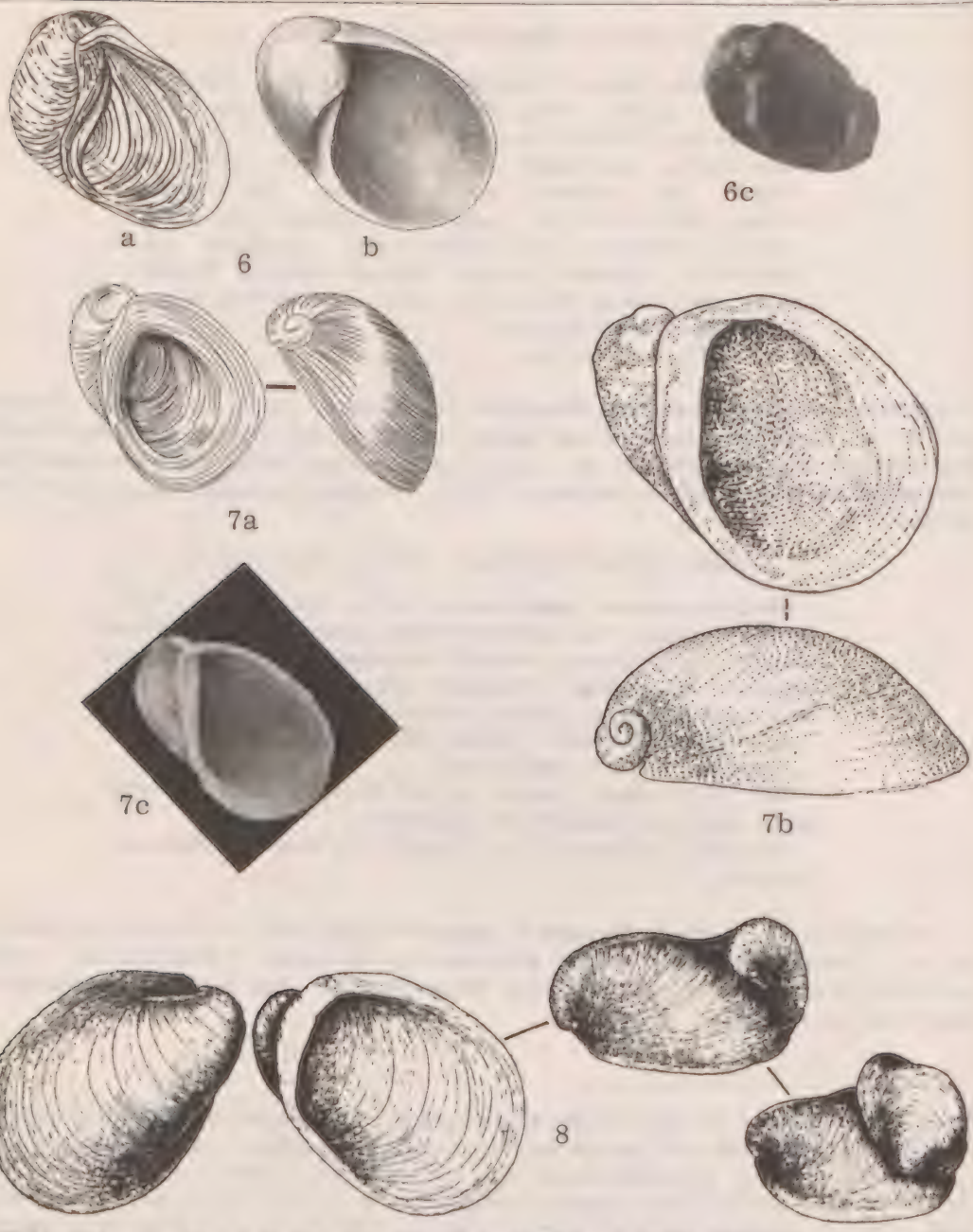
[4]There will perhaps be no end to the argumentation regarding the advisability of lumping all, or nearly all, lymnaeid species into the single genus *Lymnaea*, or whether to nomenclaturally recognize groupings of species. A compromise solution sometimes practiced is to relegate generic group names to subgeneric status, thereby, partially, conserving both views. *Lymnaea* (*Erinna*) *newcombi* and *L. aulacospira* seem to me to be distinct enough from other lymnaeid species that, for the time-being, it is convenient (to me) on practical grounds to consider them as constituting their own "species group." Likewise, *L.* (*Omia*) *onychia* and *Radix hamadai* would also seem to be related, and different from other radicine lymnaeids. However, it is still difficult to assess systematic relationships within the family because of the lack of detailed comparative information on many biological aspects of the Lymnaeidae. Only now are studies critical enough in basic detail beginning to be published.



FIGS. 6–8. Copies of some previous illustrations of *Erinna newcombi* and *Limnaea onychia*.

FIG. 6. *Erinna newcombi*. a, after H. & A. Adams (1858, pl. 138, fig. 9); b, after Thiele (1931, p 477, fig. 572); c, "type" from Hubendick (1952, p 326, fig. 16c).

FIG. 7. *Lithotis japonica* Preston and *Omia japonica* Annandale & Prashad (both = *Limnaea onychia* Westerlund). a, After Preston (1916, pl. 9, fig. 6); b, from Annandale & Prashad (1919, pl. 12, fig. 4); c, "type" from Hubendick (1951, pl. 3, fig. 5).

FIG. 8. *Lymnaea onychia* Itagaki ("large form"). From Itagaki (1959, pl. 29, fig. 1; pl. 32, fig. 26).

Erinna [Adams, 1855, p 120]

Shell semiglobose, thin, horny, olivaceous, longitudinally finely striated; spire very short, obtuse, apex rather eroded, last whorl ventricose, aperture large semiovate; inner lip posteriorly ascending on the body-whorl; columella straight excavated and with a curved elevated ridge outside the excavation, continued in front into the outer lip, which is thin and simple.

Omia [Annandale & Prashad, 1918 (1919), p 460-461], Fig. 7b.

A genus of the family Limnaeidae consisting of species in which the shell is dextral, small, thin and neritiform. The spire is short, flattened and lateral in position, the body-whorl large, ovoid, convex above and flattened on the ventral surface. The aperture, though little expanded, is relatively of great size, oval, with its main axis practically at right angles to that of the spire. The columellar fold is broad, flattened and turned slightly inwards, running obliquely across the posterior margin of the aperture and almost forming a septum in the posterior part of the shell.

The soft parts apparently resemble those of *Limnaea*, except that the tentacles are long and cylindrical or subcylindrical; the mantle is incapable of being expanded over the shell and is not thickened or highly vascular at its lower margin.

The upper jaw and radula exactly resemble those of *Limnaea*.

Type-species. *Lithotis japonica*, Preston, from Lake Biwa in Japan. [=*Limnaea onychia* Westerlund 1883].

[*Omia* Annandale & Prashad 1919 (*J. Asiatic Soc. Bengal*, n.s., 14(9): 460), Mollusca, Gastropoda, is preoccupied by *Omia* Hübner 1821 (*Verzeichniss bekannter Schmettlinge*, p 244), Lepidoptera, Noctuidae. Therefore, *Biwakoia* n. nom. (Type species: *Limnaea onychia* Westerlund 1883 = *Lithotis japonica* Preston 1916) is herewith proposed as a replacement for *Omia* as a generic-group name in the Lymnaeidae.]

SYSTEMATIC RELATIONSHIPS

Annandale & Prashad (1919) considered the Japanese *Omia japonica* [=*Limnaea onychia*] to be closely related to *Limnaea brevispira* von Martens from Sumatra, and included the latter in their genus *Omia*. This suggested relationship seems not to have received further serious consideration, and Benthem Jutting (1946b) specifically dealt with the question of *L. brevispira's* relation to *Omia* (although part of her comparison related to Annandale & Prashad's inaccurate description of *O. onychia's* tentacles and mantle margin). However, possible systematic relationships between *L. onychia* and the Hawaiian *Erinna newcombi* have been pointed out on several occasions, and because of shell similarities, Thiele (1931) considered *Omia* as a section ("Sectio") of the subgenus *Erinna* s.s.,[5] and Zilch (1959) considered *Omia* as a subgenus of *Erinna*. Hubendick (1951, p 166) said that, "The shell of *Omia* corresponds in every respect to that of *Erinna* Adams

[5]Thiele's statement, "*E.* (*O.*) *japonica* (PRESTON) in Japan und Sumatra," has been corrected by Benthem Jutting (1946a). *Lithotis japonica* Preston 1916 (=*Limnaea onychia* Westerlund 1883) is endemic in Lake Biwa and does not occur elsewhere. Because of the very reduced spire of *Limnaea brevispira* Martens 1897, Annandale & Prashad (1919) included that species in their new genus, and listed the "*known geographical range*" of *Omia* as "main island of Japan [Honshu]; Sumatra." However, there is no evidence to suggest that *L. brevispira* is closely related to *L.* (*O.*) *onychia;* to the contrary, it would seem that this Sumatran species is more probably related to or belongs with the *Austropeplea* species complex of its own geographical region.

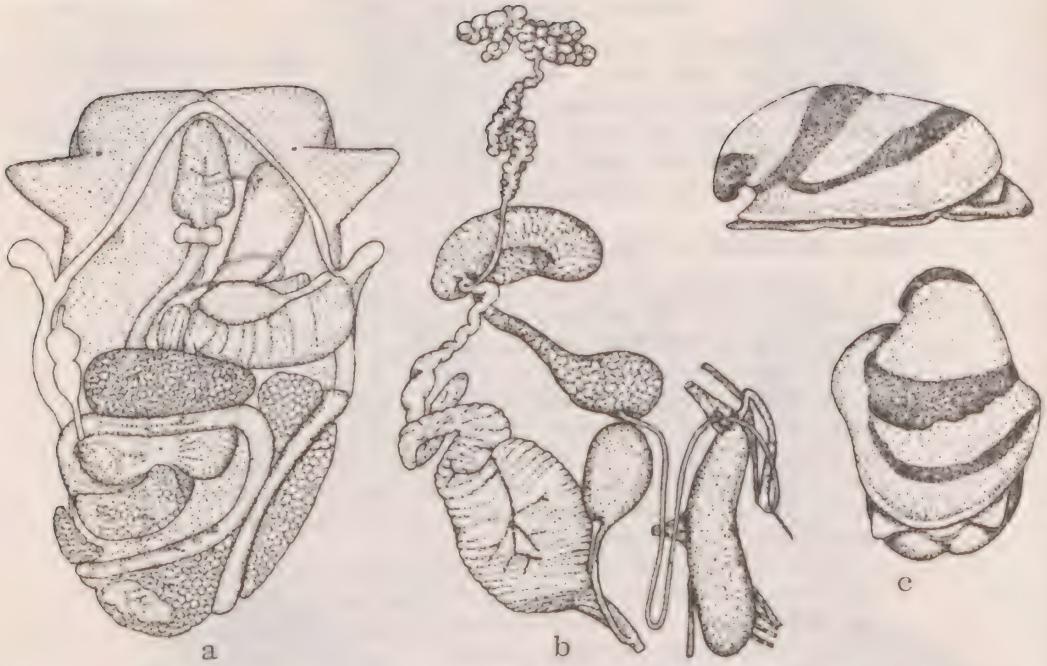
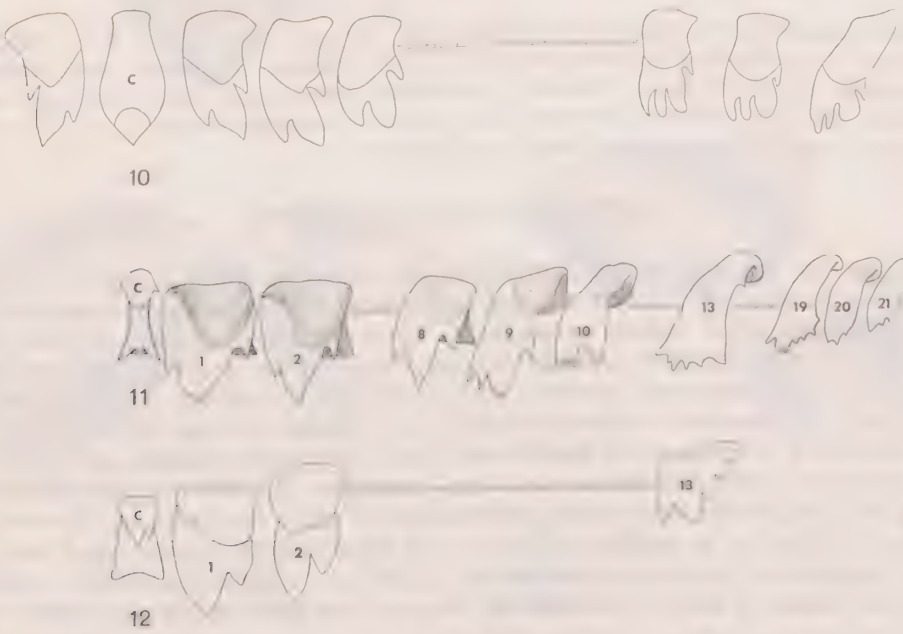


FIG. 9. Anatomy of *Lymnaea (Omia) onychia*, "large form" (from Itagaki, 1959). a, Aspects of gross anatomy; b, reproductive tract (ps = penis sheath); c, mantle (showing pigmentation) and head-foot.



FIGS. 10-12. Radular teeth. [Numbers on the individual teeth refer to their consecutive positions in their particular row as numbered from left to right after the central tooth (c).]

FIG. 10. Radular teeth of *Omia japonica* Annandale & Prashad (= *Limnaea onychia* Westerlund). After Annandale & Prashad (1919, p 461, fig. 2).

FIG. 11. Radular teeth of *Lymnaea (Omia) onychia* Itagaki ("small form"). After Itagaki (1959, pl. 29, fig. 8).

FIG. 12. Radular teeth of *Lymnaea newcombi* Hubendick. After Hubendick (1952, p 319, fig. 11e).

from Hawaii."

Characters of the soft parts of *Omia japonica* [=*Limnaea onychia*] have been mentioned briefly by Annandale & Prashad (1919), "In most respects, so far as it is possible to express an opinion on the basis of such material [extracted dried animal from the type specimen], the soft parts bear a very close resemblance to those of *Limnaea*, except that the tentacles are elongate and cylindrical." But, according to Thiele (1931), in *Erinna* and its section *Omia*, "Tier ähnlich wie bei *Lymnaea*...," and Hubendick (1951) [who also looked at extracted dried animals, but softened in a concentrated solution of sodium carbonate] concluded that the tentacles were of the "ordinary type" found in the Lymnaeidae, as was also the mantle border. Itagaki (1959) studied 2 populations of *L.* (*O.*) *onychia* from Lake Biwa, one comprising specimens of normal size, and the other population consisting of a larger form (Figs. 8 and 9). He concluded that this species should be assigned to the genus *Lymnaea* [s.l.], but separated from other species as the subgenus *Omia*. Burch et al. (1964) assigned *L. onychia* to the generic group *Radix*, mainly because of its chromosome number (n=17).

In addition to shell similarities, stressed by Hubendick (1951) and used for close taxonomic placement by Thiele (1931) and Zilch (1959), Hubendick (*op. cit.*) reported bicuspid lateral radular teeth for both *Lymnaea* (*Erinna*) *newcombi* (Fig. 12) and *L.* (*Omia*) *onychia*, but emphasized the different rounded cusps of the marginal teeth of *L.* (*O.*) *onychia*. Hubendick (1952) concluded that, "It is...impossible to decide [from information at hand] whether *L. onychia* and *L. newcombi* are closely related or have evolved independently." On the other hand, Annandale & Prashad (1919) reported tricuspid lateral teeth for *L.* (*O.*) *onychia* (Fig. 10), and Itagaki (1959) found tricuspid lateral teeth in the small shell form of this species from Kitayamada (Fig. 11), although the large form from Chikubu-jima had "...laterals ...with 1 usually, occasionally 3 cusps." I have also found tricuspid lateral teeth in *L.* (*O.*) *onychia*.

Hubendick (1951) did not describe the reproductive structures of *Lymnaea* (*Omia*) *onychia*, but he did (1951, 1952) describe them for *L.* (*Erinna*) *newcombi* (Fig. 13). For the latter he said, "The anatomical features of *L. newcombi* are similar to those of *aulacospira* ["...characterized by a comparatively short and thick penis sheath, a long spermathecal duct and an unfolded prostate]. The penis sheath and the penis, however, seem to be shorter in *L. newcombi*." Itagaki (1959) described a longer and narrower penis sheath in *L.* (*O.*) *onychia* (Fig. 9b), and Burch & Habe (unpubl.) found a relatively very long penis sheath for *L.* (*O.*) *hamadai*.

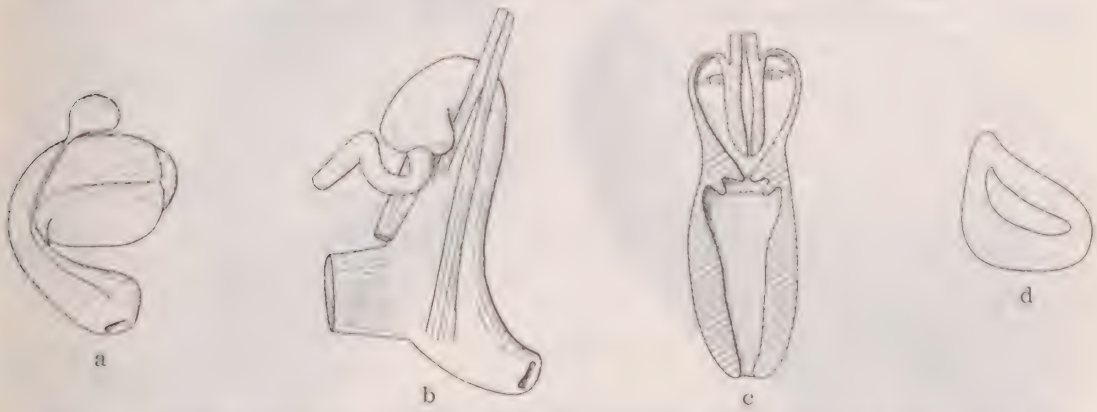


FIG. 13. Reproductive structures of *Erinna newcombi*, from Hubendick (1951, p 101, fig. 282; p 103, fig. 292). a, Terminal female genitalia; b, terminal male genitalia; c, reconstruction of longitudinal section of terminal male genitalia; d, cross section of prostate gland.

SHELLS

The shells of *Lymnaea* (*Erinna*) *newcombi* of Hawaii and *L.* (*Omia*) *onychia* of Japan are similar in that both have extremely reduced spires, with correspondingly enlarged body whorls. Although on precursory examination the shells of the 2 species seem to be the same, a more critical look reveals that they are not identical, but show some striking differences, especially in regard to shell sculpturing. But, there are also differences in shell shape, at least among shells of the 2 populations that I studied. For example, the shells of *L.* (*O.*) *onychia* are relatively more narrow than *L.* (*E.*) *newcombi;* the latter have a squat appearance. Also, the columellar portion of the shell is wider in *L.* (*E.*) *newcombi*, forming a relatively broad shelf. From the dorsum, the apical whorls of *L.* (*E.*) *newcombi* (Fig. 16a) are deflected further off-center of the longitudinal body whorl axis than

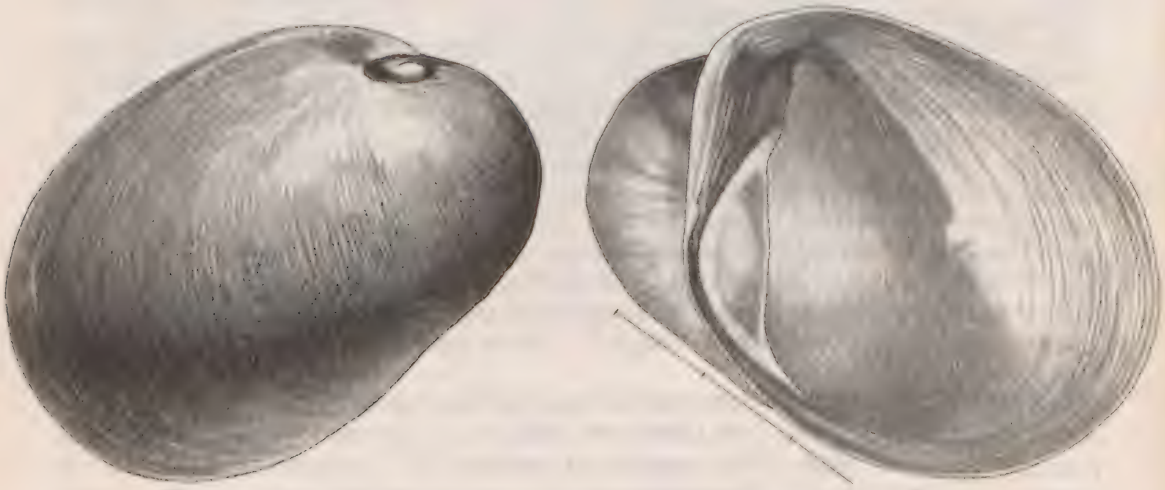


FIG. 14a. Shell of *Erinna newcombi*, dorsal and apertural views (BPBM No. 15571), from Hanakapiai Stream, Kauai Island, Hawaii. Scale line in mm.

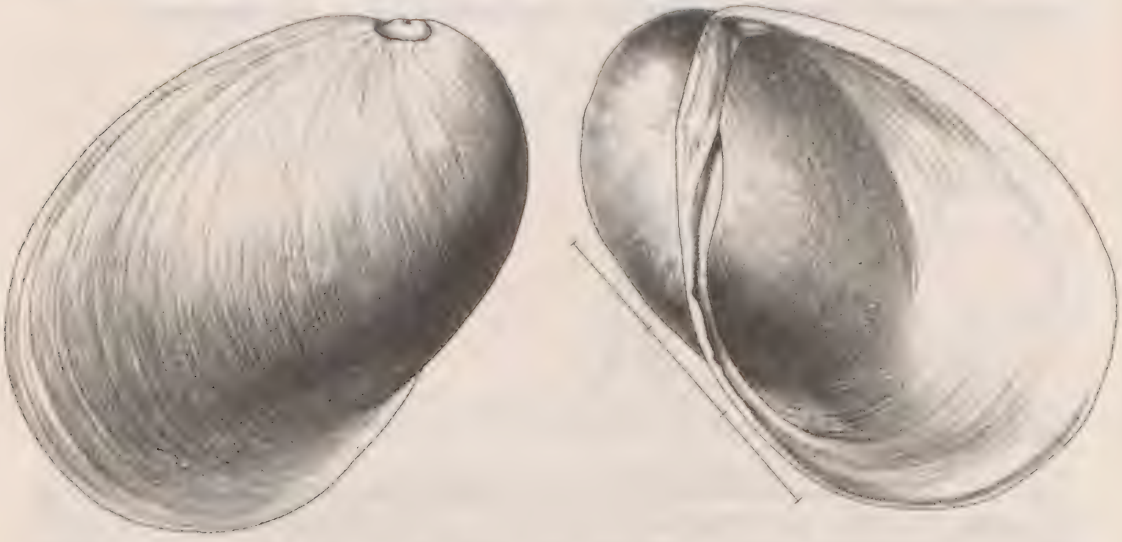


FIG. 14b. Shell of *Limnaea onychia*, dorsal and apertural views, from Lake Biwa at Otsu, Honshu Island, Japan. Scale line in mm.

are those of *L.* (*O.*) *onychia* (Fig. 16b).

Material examined. *Lymnaea* (*Erinna*) *newcombi* [courtesy of Yoshio Kondo], collected on Kauai Island, Hawaiian Islands, by C. M. Cook, Jr., from Hanakapiai Stream, at the edge of the water on overhanding rocks near swift water, 13-15 July 1907 [Bernice P. Bishop Museum No. 15571]. Shells of 6 specimens are shown in Figs. 14 and 15. The shell aperture is broadly oval (almost round). The central part of the parietal lip (Fig. 17,a) is usually appressed to the body whorl, but its distal ends (Fig. 17,b^1 and b^2) are free. There is no umbilicus, but where the parietal lip is reflected over the ventral body whorl there is sometimes an "umbilical chink" (Fig. 17,c). The apertural columella is not twisted into a plait, but forms a broad shelf (Fig. 17,d) in its terminal apertural portion. Sometimes this shelf is indented by erosions. The posterior or apical portion of the whorls (in the area of the suture with the preceding whorl) have a tendency to be shouldered (Fig. 17,e). An exaggeration of this shouldering in the body whorl gives the posterior (right) palatal lip (near the suture) a flared-out appearance (Fig. 17,f). The sutures (Fig. 17,g) are deeply impressed. The shell surface sculpture consists of distinct transverse, more or less uniform wrinkles, and superimposed spiral sculpturing reminiscent of the North American "*Stagnicola palustris elodes*" group (Fig. 18a). The "valley" between 2 consecutive wrinkle-ridges is an acute crease. Aside from its neritiform shape, the transverse sculpture is the most distinctive shell characteristic of this species. It and the spiral sculpture can be seen best under transmitted light in shells cleaned with sodium hypochlorite ("Clorox") (cf. Walter, 1962). The color of such a cleaned shell is translucent amber, with a reddish or chestnut cast in areas where the shell is thickened (e.g., in the shell apex and portions of whorls near the sutures).

Lymnaea (*Omia*) *onychia*. Collected by the author and Tadashige Habe from Lake Biwa at Otsu, August-October, 1963. Shells of 6 specimens are shown in Figs. 14 and 19. The shell aperture is more narrowly oval than that of *L.* (*Erinna*) *newcombi*, especially in its apical portion, giving the aperture a tear-drop shape. The parietal lip is usually appressed to the body whorl, as in *L.* (*E.*) *newcombi*, but it is generally more closely appressed than in that species, and the distal ends of the parietal lip are not free, or only for a very small portion. There is no umbilicus, although rarely there is a slight "umbilical chink" where the parietal lip is reflected over the ventral body whorl. The apertural columella is not twisted into a plait, and it is much narrower than in *L.* (*E.*) *newcombi*. There is a tendency for the terminal columella to form a shelf, but this is very narrow and essentially rudimentary as a "shelf." The whorls are not shouldered, or if any should be considered shouldered, then the shouldering is very narrow and minor. Therefore, the aperture does not flare out in its posterior (right) palatal portion. The sutures are impressed as in *L.* (*E.*) *newcombi*, but perhaps not as deeply set as in that species. The shell surface sculpture consists of an irregular transverse "striation" in the line of growth of the shell (Fig. 18b); it is not the close-set transverse wrinkle-striation of *L.* (*E.*) *newcombi*, but it is similar to the sculpturing of many radicine lymnaeids. There are occasional sparse indications of spiral sculpture, also evident in other radicines, but not the intense spiral "striation" which characterizes many species of "*Stagnicola*." The color of the shell of *L.* (*O.*) *onychia* is pale translucent yellow.

DISCUSSION

On superficial shell characters, the Hawaiian and Japanese neritiform lymnaeid species would seem to be related, and indeed, past works have included the 2 in

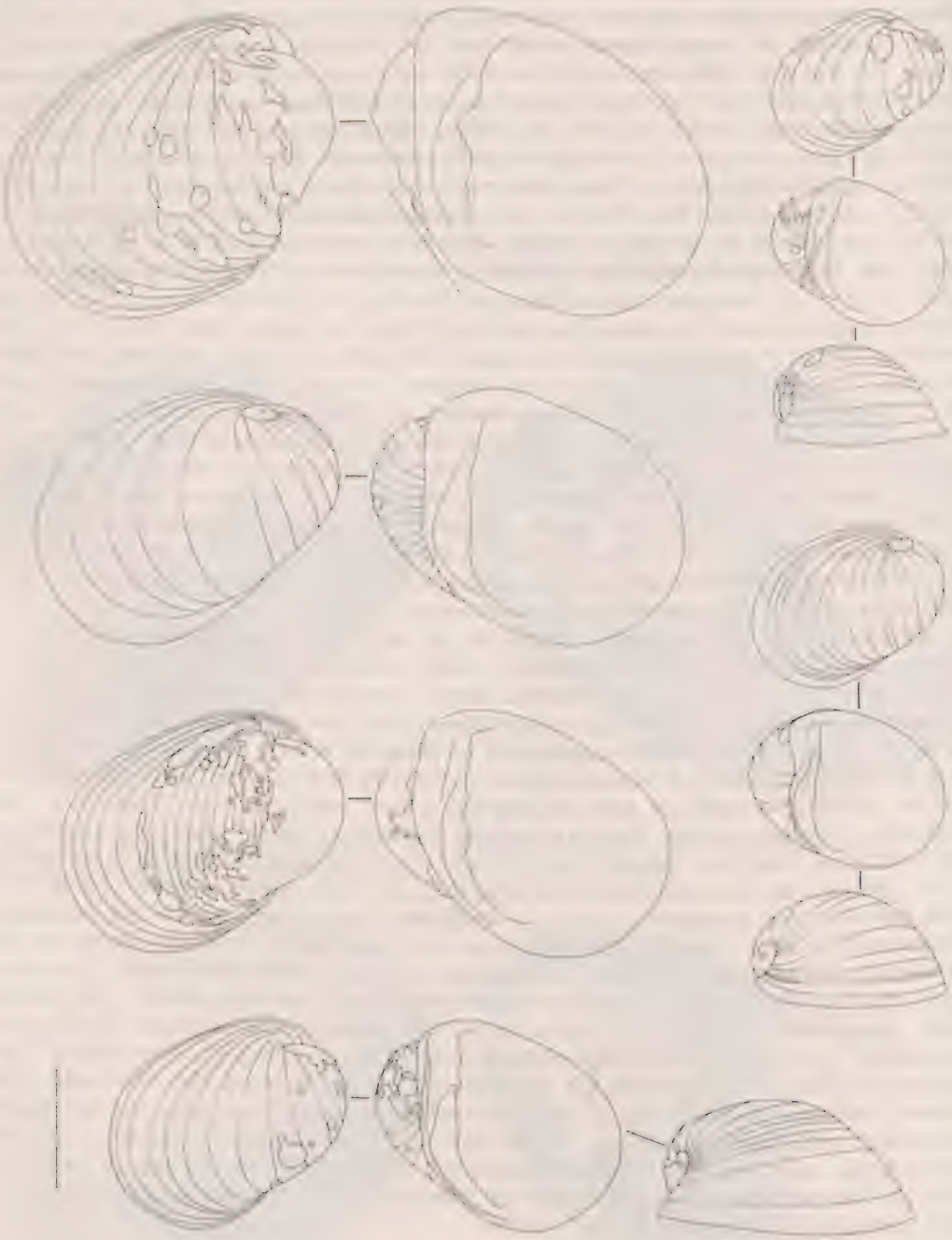
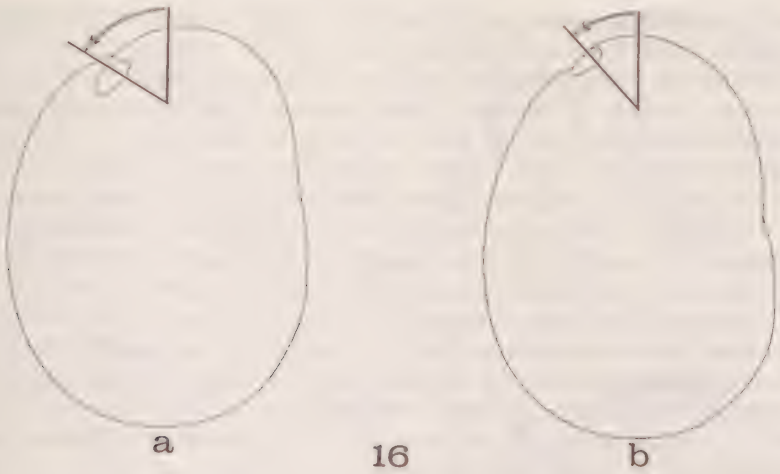


FIG. 15. Shells of 6 specimens of *Erinna newcombi* (BPBM No. 15571), from Hanakapiai Stream, Kauai Island, Hawaii. Scale line in mm. Several shells are noticably erroded. Lines on shells are not intended to indicate sculpture *per se*, but are drawn at intervals only to indicate direction of transverse shell sculpture.



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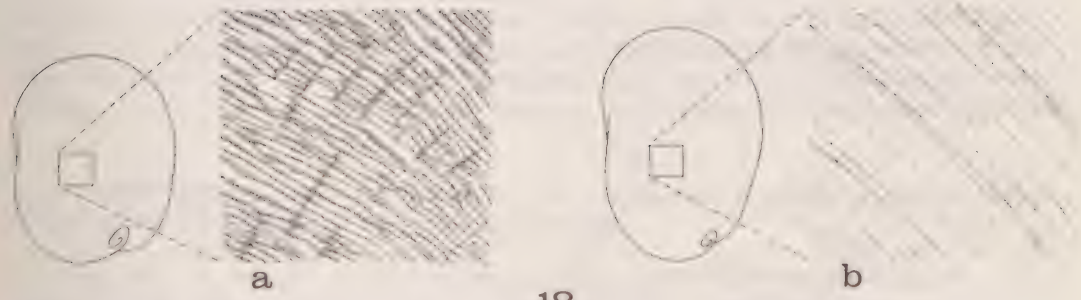

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FIGS. 16–18. Shell characteristics of *Erinna newcombi* and *Limnaea onychia*.

FIG. 16. Diagrams showing the angle of deflection of the apex from the longitudinal axis of the body whorl of a, *Erinna newcombi*, and b, *Limnaea onychia*.

FIG. 17. Shell parts (see text, p 23).

FIG. 18. Shell surface sculpture of a, *Erinna newcombi*, and b, *Limnaea onychia*.

FIG. 19. Shells of 6 specimens of *Limnaea onychia* from Lake Biwa at Otsu, Honshu Island, Japan. Scale line in mm. Lines on shells are not intended to indicate sculpture *per se*, but are drawn at intervals only to indicate direction of transverse shell sculpture.

the same restricted species group. However, closer inspection of the shells of the Hawaiian and Japanese species shows that they are not identical in every respect, and in fact, they are particularly different in shell sculpture. *Lymnaea* (*Omia*) *onychia* has a relatively smooth shell, especially similar to species of the *Radix* group, but *L.* (*Erinna*) *newcombi* has a fine, but very distinctive shell sculpture, which can be distinguished as "fine" only in absolute terms, and not relative to its own shell size. Such a shell sculpturing is not known to me to occur on any other lymnaeids, except *L.* (*E.*) *aulacospira*,[6] also of Hawaii.

I have not been able to observe the radular teeth of *Lymnaea* (*Erinna*) *newcombi*, but Hubendick (1951, 1952) says the laterals are bicuspid. However, the lateral teeth of *L.* (*Omia*) *onychia* are clearly tricuspid rather than bicuspid, which is of some significance since no n=17 (haploid chromosome number) species is known that has bicuspid lateral teeth (*L. onychia* has 17 pairs of chromosomes; Burch, et al., 1964).[7] At this time, it is difficult to assess systematic importance of the round-cusped marginals shown for *L.* (*O.*) *onychia* by Annandale & Prashad (1919) and Hubendick (1951), and for *L.* (*O.*) *hamadai* by Burch & Habe(unpubl.). (All of the marginal teeth of *L.* (*O.*) *onychia* do not show this condition.)

In regard to morphology of soft anatomy, Hubendick (1952) stresses the condition of the prostate gland as a taxonomic character, and shows a peculiar unfolded prostate gland for *Lymnaea* (*Erinna*) *newcombi*, as well as for the Hawaiian species *L.* (*E.*) *aulacospira* and *L.* (*Pseudisidora*) *reticulata*.[8] A similar unfolded prostate gland for non-Hawaiian species has been reported by him only for the North American *L.* (*Pseudosuccinea*) *columella* and *L.* (*Bakerilymnaea*) *bulimoides*, the South American *L. viator* and *L. peregrina*, and the European *L. glabra*. Itagaki (1959) shows a prostate gland with a well-developed fold in *L.* (*O.*) *onychia*, which I have confirmed (unpublished).

Limnaea onychia has the following characteristics in common with many Eurasian lymnaeids, especially those species that are often considered to comprise the genus *Radix:* an unifolded prostate gland, tricuspid lateral teeth, a small and/or thin penis and sheath (relative to the praeputium), 17 pairs of chromosomes, and a relatively smooth shell with little microsculpture.

Erinna newcombi, on the other hand, has an unfolded prostate gland, bicuspid lateral teeth, a relatively large and/or thick penis and sheath, and a shell with well-impressed and characteristic sculpturing. Its chromosome number has not been determined, but its related species, *E. aulacospira*, has 18 pairs of chromosomes, and, judging from the conservativeness of lymnaeid chromosome numbers at the species level, *E. newcombi* probably also has 18 pairs of chromosomes.

Walter (1969), in the introductory section preceeding his detailed study of the

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[6] H. J. Walter (pers. comm.) also considers the sculpture of *L. aulacospira* to be unique among lymnaeids. He has not observed *L. newcombi*.

[7] *L. aulacospira* of Hawaii is also reported by Hubendick to have bicuspid laterals, and I have found this species to have 18 pairs of chromosomes. To my knowledge, no lymnaeid species with bicuspid laterals has less than 18 pairs of chromosomes.

[8] Hubendick (1952) reported the Hawaiian species *Lymnaea* (*Pseudisidora*) *volutata* and *L. rubella* to have unifolded prostate glands, but this needs to be confirmed, since all of his illustrated shells of "*L. volutata*" appear to belong to the introduced Oriental *L.* (*Austropeplea*) *ollula*, which he does not mention as occurring in Hawaii. His "*Lymnaea rubella*" may also have contained specimens of *L. ollula*. The occurrence of *L. ollula* in the Hawaiian islands has been documented by Alicata & Swanson (1937) and Alicata (1938).

anatomy of the North American *Lymnaea* (*Stagnicola*) *catascopium*, regards "...most of the Hawaiian [lymnaeid] species...[to be]...advanced stagnicoline in character." Further particulars were not published, but in view of his very detailed study of *L. catascopium* and his wide experience with lymnaeids in general, serious consideration must be given to this suggestion. More detailed studies will be published, no doubt, by Walter in the future.

Inasmuch as shell shape in lymnaeids is considered to be influenced and affected by environment, it is of some pertinence to mention the habitats of the Hawaiian and Japanese neritiform lymnaeids. *Lymnaea* (*Erinna*) *newcombi* lives on the Island of Kauai on rocks in swiftly flowing water, usually on the nearly vertical faces of waterfalls.[9] The Japanese *L.* (*Omia*) *onychia*, although living in a lake, is also conditioned to turbulent water, clinging to rocks near the shore where they are subject to considerable wave action. It seems obvious that the shell shapes of these 2 species are the adaptive results of the turbulent water habitat in which they both evolved, and there would seem to be serious doubt that they are closely related.

If the Hawaiian islands are truly oceanic islands, as contended by Zimmerman (1948), and not part of a sunken mid-Pacific continental land mass as suggested by Pilsbry (1900), then a question of considerable interest is, "From *where* did the original lymnaeid colonizers come?"

Some bearing on this question are the following observations:

1) *Lymnaea* (*Erinna*) *aulacospira*, related to *L.* (*E.*) *newcombi* and probably also to other endemic Hawaiian species, is a n=18 chromosome species with bicuspid lateral teeth; species with either of these characters are not known to occur naturally in the rest of the Pacific, Japan, Australasia, Southeast Asia, India or Africa.
2) Walter (1969) considers Hawaiian lymnaeids to be "advanced stagnicoline" in character, and that the advanced stagnicolines evolved in North America. Advanced-stagnicoline species are known from North and South America and Europe.[10] None are definitely known from the rest of the Pacific, Japan, Australasia, Southeast Asia, India or Africa.

Therefore, it seems likely that the zoogeographical relationships of the Hawaiian lymnaeids point to the Western hemisphere (North and/or South America),[11] rather than to the rest of the Pacific, Australasia, the Orient, or Asia in general. The similarly shaped shells of *Lymnaea* (*Erinna*) *newcombi* of Hawaii and *L.* (*Omia*) *onychia* of Japan are undoubtedly due to parallel evolution, and not to a common ancestor.

ABSTRACT

The 2 neritiform lymnaeids, *Erinna newcombi* H. & A. Adams of Hawaii and *Limnaea onychia* Westerlund of Japan, which are often placed in the same species group or genus because of their similar shell shapes, do not seem to be closely related. Their similar shell shapes, apparently adaptations to their turbulent

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[9] Hubendick's statement (1952, p 327) that "The different [Hawaiian lymnaeid] species are not restricted to different islands or different parts of the islands or even to different types of habitats," obviously does not apply to *L. newcombi*.

[10] Poland (*L. occulata* Jackiewicz, 1959), although Walter (1969) suggests that this species may have been introduced from North America ("*L. caperata* Say?").

[11] See Addendum, p 30.

water habitats, are undoubtedly due to parallel evolution and not to a common ancestor. *L. onychia* is related to the Eurasian radicine species complex, and *E. newcombi* most likely had a western hemisphere (North and/or South America) ancestor.

ACKNOWLEDGEMENTS

I wish to thank Dr. Yoshio Kondo of the Bernice P. Bishop Museum, Honolulu, for sending me the specimens of *Lymnaea* (*Erinna*) *newcombi*, and Dr. Tadashige Habe, National Science Museum, Tokyo, for taking me to collect *L.* (*Omia*) *onychia*. I wish also to acknowledge my colleagues, Drs. J. P. E. Morrison and H. J. Walter, for many informative and fruitful discussions on the Lymnaeidae, although they do not necessarily agree with all aspects of this paper. Figures 1-5, 14, 15 and 19 were kindly drawn by Mr. John L. Tottenham.

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ADDENDUM

After this paper was set in type, I received the manuscript from Joseph P. E. Morrison entitled "Notes on Hawaiian Lymnaeidae" (MALACOL. REV., 1: 31-33). Dr. Morrison also points out the significance of the bicuspid lateral radular teeth of the endemic Hawaiian lymnaeids, and suggests that they ". . . evolved from the North American (Alaskan) or Holarctic (*Stagnicola*) stock introduced by chance by bird migration over geologic time."

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NOTES ON HAWAIIAN LYMNAEIDAE

J. P. E. Morrison

The Hawaiian Lymnaeidae have been treated in various previous publications, the most recent and comprehensive being that of Hubendick (1952). However, the latter report is seriously incomplete in 3 very important particulars. (1) Regardless of that author's desire to have only 1 genus *Lymnaea* in the family, he completely omitted the pertinent named subdivisions that indicate the known relationships of the various species. With very few exceptions the anatomically and physiologically supported groups of Lymnaeidae can be distinguished by shell characters alone, whenever animals are not available for study. (2) Hubendick was apparently unaware of the publications by Alicata & Swanson (1937) and by Alicata (1938) on the role played in the life history of the cattle fluke in Hawaii by the introduced species *"Fossaria ollula"* (= *Galba viridis* Quoy & Gaimard). (3) The origin of the Hawaiian lymnaeid fauna was obscured by Hubendick's failure to recognize any subdivisions of *Lymnaea, sensu latu.*

NATIVE HAWAIIAN LYMNAEIDAE

There are 2 native, endemic (pre-Polynesian) generic groups of Lymnaeidae known from the Hawaiian Islands. These are *Erinna* and *Pseudisidora.* The radular characters (i.e., bicuspid lateral teeth) indicate that both these groups evolved from North American (Alaskan) or Holarctic (*Stagnicola*) stock introduced by chance by bird migration over geologic time.

ERINNA H. & A. Adams 1855

Type species: *Erinna newcombi* H. & A. Adams 1855

The USNM collections include material from the type lot of *newcombi*, USNM 121459, from the Lea Collection. These specimens and others at hand (USNM 20606 from Hanapepe Falls, Kauai, from the U. S. Exploring Expedition) show variation in height of spire from the maximum indicated by the lectotype (Brit. Mus. 1950-5-19-13) (figure 16c of Hubendick) to the shortest extreme, in which the spire does not project beyond, or when eroded, even reach the posterior edge of the aperture.

The presence of a 2nd species of *Erinna*, *E. aulacospira* Ancey 1889, with a moderately but definitely short spire indicates to me that there are 2 species groups of lymnaeids endemic to Hawaii, the 2 closely related species of *Erinna*, and the less closely related *Pseudisidora* complex.

PSEUDISIDORA Thiele 1931

Type species: *Lymnaea rubella* Lea 1841

Names other than *rubella* for the dextral species of this ambidextrous group include *sandwichensis* Philippi 1845, *volutata* Gould 1848, and *oahuensis* Eydoux & Souleyet 1852. These snails, ecologically fluviatile, from the rapid (mountain) streams of the Hawaiian Islands include the only sinistral species of Lymnaeidae known. *Pseudisidora producta* Mighels 1845 includes as a synonym *Physa reticulata* Gould 1847. Mighels' brief description and published measurements exactly fit this species. The "type specimens" of *reticulata* Gould, figures 16 d-f of

Hubendick (Brit. Mus. 42-1-22-509), may be paratypes if with them there is a printed Smithsonian Institution label such as was distributed with Smithsonian Institution duplicates in the time of P. P. Carpenter (ante 1870). The holotype of Gould's *Physa reticulata*,, USNM 5540 (badly broken), and paratypes, USNM 20710 and MCZ 216770, are recorded in Johnson (1964, p 139).

I have not seen specimens of the short-spired sinistral species named *"Physa" umbilicata* Mighels 1845 and *Lymnaea affinis* Eydoux & Souleyet 1852. Synonyms of this second sinistral species include *"Physa" peasei* Clessin 1886 and *"Physa" naticoides* Clessin 1886.

INTRODUCED HAWAIIAN LYMNAEIDAE

GALBA Schrank 1803[1]

Type-species: *Lymnaea truncatula* Müller 1774

Critical study of the radular figures and anatomical details of the male organs figured, as well as the shells, indicate that *Lymnaea volutata* Hubendick 1952 (not of Gould) is actually the species *Galba viridis* Quoy & Gaimard 1833. This is the intermediate host of the cattle fluke (*Fasciola gigantica*) reported as *Fossaria ollula* Gould by Morrison in Alicata (1938, p 16). Now widespread in lowland wet areas of the Hawaiian Islands, it was not even recorded as present there before the late 19th century. *Lymnaea rubella* Hubendick 1952 seems to have included a mixture of the endemic *rubella* Lea, plus some specimens of *Galba viridis* Quoy & Gaimard represented by figures 5b, 5f, and 5g of Hubendick.

PSEUDOSUCCINEA F. C. Baker 1908

Type-species: *Pseudosuccinea columella* Say 1817

This North American species has been known from the Watercress area, Pauoa Valley, near Honolulu, Oahu, since at least 1952. In October of that year J. E. Alicata sent a series to the USNM for a check on the identity of this introduced species.

ABSTRACT

The Hawaiian Lymnaeids include 2 endemic groups derived from *Stagnicola* stock.

1) *Pseudisidora* species (dextral and sinistral)
2) *Erinna* species (short spired)

The intermediate host of the cattle fluke in Hawaii, *Galba viridis* Quoy & Gaimard, was introduced about 1890 from the East Asiatic region.

The North American *Pseudosuccinea columella* Say was accidentally introduced to Hawaii about 1950.

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MORPHOLOGICAL FEATURES OF LIBERIAN *BULINUS* AND *B. TRUNCATUS* OF EGYPT: A PICTORIAL ESSAY ON SNAILS OF THREE SUBGENERA (PLANORBIDAE: BASOMMATOPHORA)[1]

Harold J. Walter[2]

On consideration of the confusingly complex morphogenetic, biomedical problem overshadowing attempts to classify snails that are carriers of schistosomiasis and to evaluate their remarkable biotic potentials, we can anticipate only very limited confirmed successes in these endeavors unless much further accurate and convincing morphological data accumulate in the presently deficient literature. This investigation is dedicated to that proposition.

Most of the data given here were obtained in Liberia from 1959 to 1961 in laboratory studies integrated with field investigations made by me on the distribution, ecology and population dynamics of *Bulinus* and *Biomphalaria* species. Were it not for excellent laboratory facilities at Harbel, and for the field station at Voinjama, provided by the Liberian Institute for Tropical Medicine in proximity to field populations of the snails, essential phases of this morphological investigation could not have been carried out. Facilities provided by the Museum of Zoology of the University of Michigan were important to the completion of the research.

This and some of my related publications owe a great deal to the efforts of Dr. J. B. Burch, and I gratefully acknowledge his assistance at this time. For his role in the initiation and support of this project, Dr. Henry van der Schalie deserves special thanks. Dr. Roland Hauck, when with the Firestone Rubber Plantations Company at Harbel, spiritedly gave scientific aid that is much appreciated. Dr. (and Mrs.) Charles Jones, and Dr. (and Mrs.) George Harley, formerly of the Suakoko Agricultural Station, and of the Ganta Methodist Mission, respectively, graciously provided accommodations important to field work in the hinterland, during which I depended much on the guidance of my chief Liberian aide, Shakespeare Williams. He, and aides John Gibson, Samuel Vonleh, and Henry Stephenson repeatedly risked infection with schistosomiasis, in my service. Others to whom I am indebted for vital aid during a long struggle to keep the publication effort from aborting, are Dr. J. Allen Scott, Mrs. Herma Van Bomel, Mrs. Arthur Honeyman, and Mrs. Elizabeth Smith. The ready cooperation and long-continued funding of my investigations by the National Institutes of Allergy and Infectious Diseases is acknowledged with great appreciation.

In respect to pertinent literature of exceptional importance, I wish to call attention to the superb, pioneering, biomorphological work of Larambergue (1939a) on *Bulinus contortus* Michaud (=*B. truncatus* (Audouin)), and to the series of publications of Burch and his colleagues (see References, p 88) on chromosomal and immunological characteristics of *Bulinus* species.

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NOTE ON THE CONTENT OF THE FIGURES

The anatomical data were obtained entirely through the use of simple dissection technique and temporary microscope-slide mounts. The small size of *Bulinus forskalii* limited study of certain of its parts, but it facilitated study of other of its parts by transmitted light at higher magnifications. For related reasons this species is adopted for introducing anatomical generalities and the scheme of standardization that is employed in pictorializing all 3 species. Great effort was made to be exceedingly accurate wherever possible. However, an inevitable margin of drawing error is involved, while in recording and collating the mass of data obtained and in abstracting the information given here as re-scaled drawings, minor discrepancies appeared, and some possible uncertainties about measuring errors were not resolved. With this reservation, the scales indicated for the figures otherwise may be taken as being precise. Almost every figure is based on large scale drawings - "optical tracings" - made with the aid of a Leitz light-polarizing drawing apparatus. The study left little doubt that only 2 species of Bulininae exist in Liberia.

The materials presented here are in 4 parts, the first three on reproductive anatomy, as follows:

PART I. *Bulinus* (*Pyrgophysa*) *forskalii*)p 37),
PART II. *Bulinus* (*Physopsis*) *globosus* (p 48),
PART III. *Bulinus* (*Bulinus*) *truncatus* (p 66),
PART IV. Morphology of body, teeth and shell of all three species (p 77).

PART I.

Liberian *Bulinus* (*Pyrgophysa*) *forskalii* (Ehrenberg). Reproductive Anatomy. The figures are based on collections containing about 380 specimens, obtained from 28 localities by the author, and on many laboratory-reared specimens.

FIGURE 1. The shell, reproductive system, and egg mass of *Bulinus forskalii*. The shell is from a selected specimen, while the given features of the reproductive organs represent what is judged to be most characteristic of robustly adult members of the species in Liberia, according to an analysis of many specimens. Given dimensions, including those of the egg mass, are representative of the upper range of size in the totality of examined series. Morphological sexual maturation is generally completed by the time the shell reaches 8 mm in length. The largest shell seen was 15.7 mm long. The given shell has 5 3/4 whorls, and shows periostracal "spines" on its shoulder carina. Within the dashed outline representing the egg mass, an egg capsule is shown. The female system must undergo great distention and distortion in producing such a large mass and capsule, even if possible swelling of the mass after its deposition is accounted for. A considerable blackish granular pigment is distributed throughout the reproductive system. The length of the posterior prostate may be somewhat exaggerated, but perhaps it may normally stretch to that length.

alb. gl. = albumen gland; ant. prost. = anterior prostate; carr. amp. = carrefour ampoule; f. po. = female pore; herm. d. = hermaphroditic duct; m. = male; ovo. = ovotestis; post. prost. = posterior prostate; prepu. = preputium; proov. = prooviduct; sh. = sheath; ut. = uterine. The "bursa" is the bursa copulatrix. The scale applying to the reproductive tract and egg mass also applies to Figs. 4, 7, 10, 13, 14, 16, 17, 19, 21, 26, 34, 41, 42, 45, 47-50, 52, 54, 55, 57, 65-66, 72, 77-80, 82-84, 86.

FIGURE 2. The ovotestis of the specimen represented in a, Fig. 4. Apical and adapical faces of the organ are shown, along with a cross-section. By further dissection, it was demonstrated to have about 28 or 30 acini, grouped in about 6 clusters, and a short but distinct posterior (adapical) collecting canal. Surface inspection reveals little about the orientation and identity of the clusters. ol. = outlet; 1 = An acinus of the most anterior or abapical acinus-cluster.

FIGURE 3. Structural analysis of the ovotestis of 2 specimens. Example a is shown flattened out, so as to spread the acini apart. The collecting canal (coll. c.) is slightly exaggerated. The specimen shows a contracted, constricted state of the atrium. For example b, all of its acini are shown, and the sequential position of its acinus clusters, as best as could be judged, is indicated by numbers, the 7th being the apical one. All but the first cluster, 1, opened into the collecting canal, as shown for a. Defining the sequence, and the individuality of the clusters or acini is arbitrary to some extent. The basal stalks of the clusters are shown cut through exactly where they joined the atrium or collecting canal.

Although made with the aid of a drawing apparatus, the drawings were finished freehand in such a way that the shown relative proportions among the acini are somewhat distorted. Otherwise, the scale corresponds to that for Fig. 2. The same scale with similar qualifications, also holds in respect to Figs. 30 to 33, and 67 to 69. Stippling indicates orange to red-brown clumps of granules showing through the surfaces of the acini. Specimens a and b also are represented in c and d, Fig. 4, respectively.

FIGURE 4. Hermaphroditic structures of 6 specimens representing several populations. The gonads of d, e, f, and of b in one view, are flattened out, and thereby have been somewhat distorted. That of a is frayed out somewhat from dissecting the acini apart.

Scale as in Fig. 1. Shell-lengths of the specimens, a to f, respectively (in mm): 10.0, 10.4, ca. 8.5, 9.3, 9.9 and 11.7. atr. = atrium; v-c. ti. = vascular-connective tissue; hd1 to hd5 = structural divisions of the hermaphroditic duct.

FIGURE 5. The hermaphroditic duct of specimen d, Fig. 4, untwisted and straightened out, showing its 2 morphologically differentiated faces, that on the left showing a "rachis." A cross-section is given in black silhouette. The occurrence of large, thick, pointed vesicles, along with smaller digitiform and flat, cockscomb-like ones in the regions indicated, is characteristic of the Liberian snails. The prominent bird-head-shaped vesicle at the beginning of the 3rd division of the duct is not a constant character and each specimen differs in similar details. Pustules in region 4, while minute, appear to be histologically well-differentiated. Region 5 is minutely kinky and complexly dissected by folds, over and among which lies a web-like complex of musculoconnective fibers.

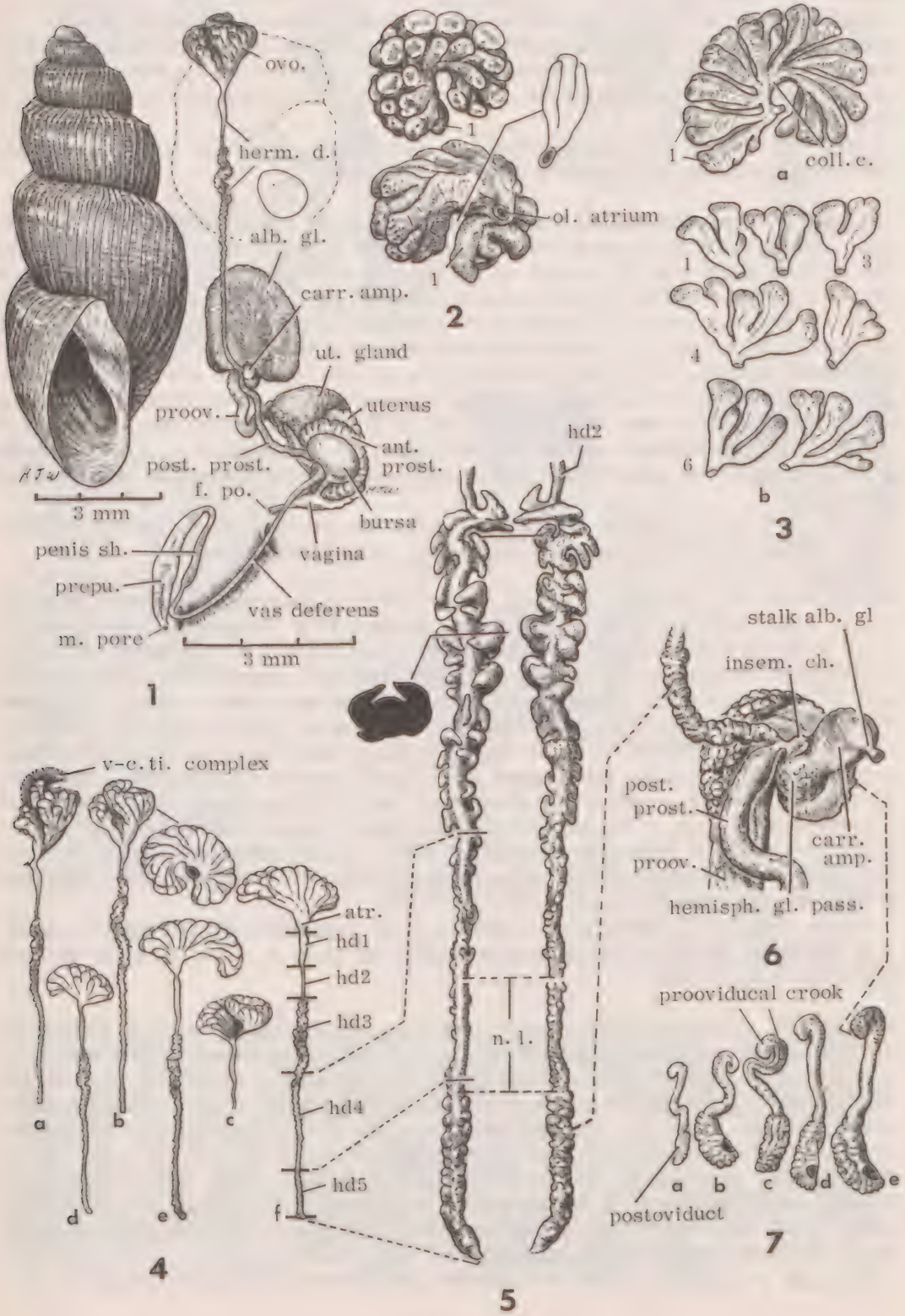
hd2 = division 2 of the hermaphroditic duct; n. l. = region in which narrowing of the lumen occurs rapidly with marked increase in the thickness of the wall of the duct.

FIGURE 6. The carrefour complex. The drawing is based on many dissections. The carrefour ampoule has been twisted upward and to the right of the figure, to reveal the seminal reservoir (unlabelled), which ordinarily is tightly sandwiched between the insemination chamber and the base of the ampoule. The chamber and the reservoir together tend to appear as a single u-shaped structure when viewed as indicated. A golden glint, from cilia, shines through the walls of this "u" and aids importantly in identifying it in dissection. The glandular passage has a thickly glandular wall and stands out among the organs because of its more pronounced yellowish color. The coarsely rugose condition of the outer curvature of the crook of the prooviduct is highly characteristic of the Liberian snails, and it represents massed glandular pustules which communicate by pitlike openings with fold-fissures of the oviducal lumen.

The terminology expresses theoretical sequential stages in reproductive processes inferred solely from the structural relationships. alb. gl. = (of the) albumen gland; carr. = carrefour; hemisph. gl. pass. = hemispherical glandular passage, whereby (theoretically) "just-albuminated," freshly inseminated egg-cells pass to the oviduct; insem. ch. = insemination chamber; post. prost. = posterior prostate; proov. = prooviduct.

FIGURE 7. The oviduct of 5 specimens, having shell-lengths, respectively, a to e, of 8.3, 10.0, 10.0, 10.4 and 11.7 mm. Several populations are represented. The last example is abnormally swollen from imbibing a relaxing solution used as a dissecting fluid. It and example d have been more or less straightened out. The others show their *in situ* postures. Scale as in Fig. 1.

FIGURE 8. The oviduct of a specimen having a shell 10.0 mm long. The ventromesial and laterodorsal faces of the postoviduct, respectively, are revealed in a and b. The internal face of the ventromesial half of that organ is shown in c, and that of the opposite half in d. Each half exhibits a large longitudinal gland-fold. These folds divide the lumen into 3 major chambers. Partly because the organ


ovo.
herm. d.
alb. gl.
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penis sh.
prepu.
vas deferens
m. pore
3 mm
3 mm
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stalk alb. gl
insem. ch.
post. prost.
proov.
carr. amp.
hemisph. gl. pass.
6
prooviducal crook
postoviduct
7

cannot be dissected away from the uterine gland without being damaged, it is represented in part as a reconstruction, somewhat generalized as to details. An anastomosing pattern of plications is shown somewhat generalized within the prooviduct, in c. A special single pathway that might conduct sperm along the length of the oviduct was not identified. The originally observed posture of the tract is indicated.

ol. = outlet of the oviduct into the uterine vestibule; pass. = opening of the hemispherical glandular passage into the oviducal crook.

FIGURE 9. The uterovaginal tract, and its topographic relationship to the postoviduct. Drawings a and b show how the postoviduct is partially sandwiched between the uterine gland and the pocket of the uterine vestibule. The oviducal outlet is placed somewhat away from the edge of the pocket. An imagined semidiagrammatic "curving cross-section," b, made where indicated by the arrow a, is shown. This pictorial device results in certain discrepancies for which the reader must allow. Indicated porelike outlets of tubules of the uterine gland, b, are somewhat conjectural. Numerous musculoid strands arise from the lateroventral wall of the uterus and pass across the anterior end of the postoviduct to join a complex of fibers partly embedded in the uterine gland, as indicated in c. These strands greatly obscure the postoviduct, and make it exceedingly difficult to dissect it out entirely.

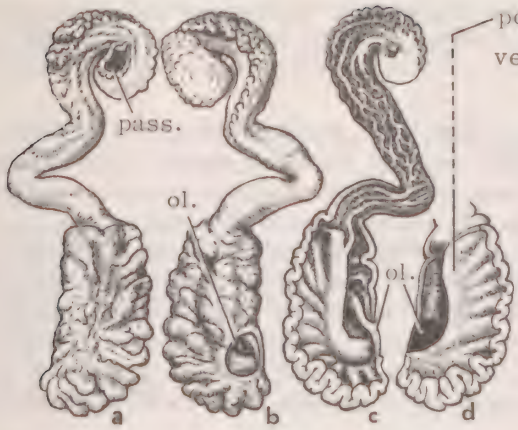
e. fs. = external fissure delimiting the uterine gland; i. fs. = internal fissure; pck. = pocket of the uterine vestibule; m. st. = musculoid strands.

FIGURE 10. The uterovaginal tract of 11 specimens representing several populations. The anterior prostate is shown in place in b. Example a was dissected away from the living animal in water, to which alcohol was subsequently added and replenished several times as it evaporated. The final result was a great shrinkage of the copulatory bursa and swelling of the remainder of the uterovaginal structures. Pronounced pustules formed on the bursa, increasingly, as it shrank. Comparable phenomena occurred in other specimens subjected to similar treatment. Specimens b, d, and i were dissected alive in a relaxing fluid; the other preparations were made from preserved snails. Examples f and g have been flattened out. Most of the represented variation in proportions is interpreted as being postural, and contingent on transient states of contractions of various muscular elements. Sometimes the vagina projects decidedly from the body wall, when it is prolonged as in h.

Scale as in Fig. 1, with some reservations as to possible errors made in handling the data. Recorded shell-lengths in mm: a, 11.7; c, 10.4; d, 11.6; e, 10.0; f, 9.0; g, 8.3; k, 10.0.

FIGURE 11. The uterovaginal tract. The drawings are based on many specimens and represent features judged to be most nearly typical. Views of the ventral, a, and dorsal, c, sides of the tract, and of the interior face of the dorsal wall, b, are shown. An indicated bright yellow external area is a conspicuous landmark demarcating the boundary of the uterine gland. Internally, the yellow color may be largely confined to 1 major fold, but extends to 3 additional folds in some specimens. The uterovaginal wall is well-ciliated overall. Fine lines diagonal and transverse to the uterus, a, indicate the arrangement of superficial muscle fibers. Sometimes the inner uterine wall between the vagina and the yellow folds is decidedly pink (in the "provaginal" region).

do. sem. = dorsal extension of a channel taken to be the seminal gutter; i. fs. =



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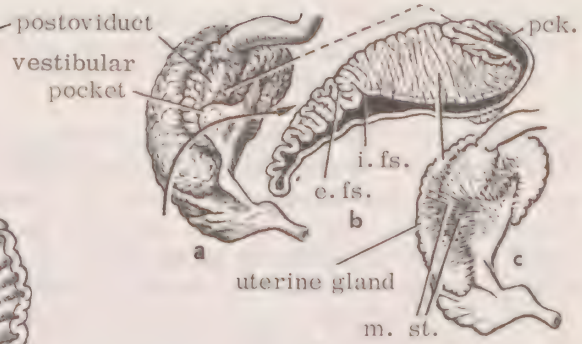

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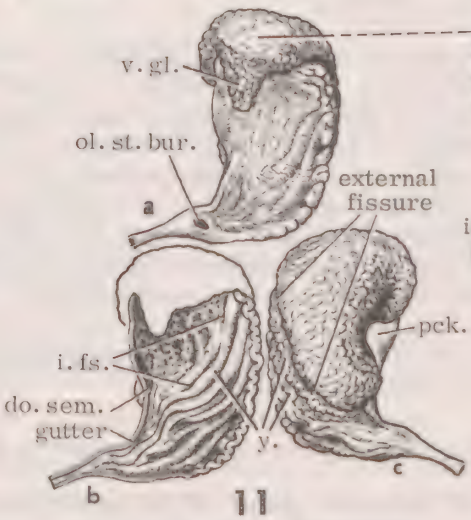

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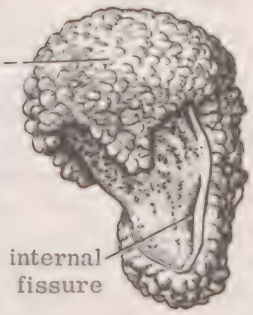

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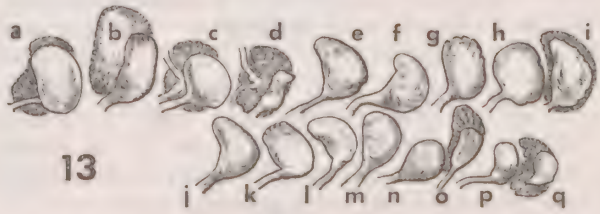

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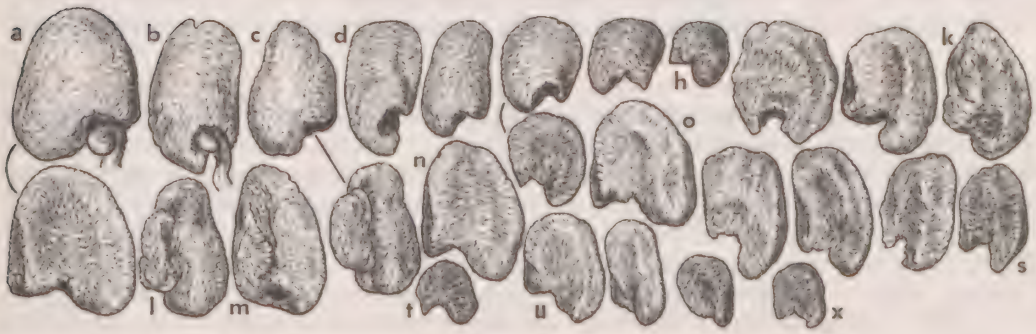

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internal fissure; ol. st. bur. = outlet of the stalk of the copulatory bursa; pck. = pocket of the uterine vestibule; v. gl. = ventral division of the uterine gland; y. = bright yellow tissue.

FIGURE 12. The uterine gland of a specimen having a shell-length of 9.4 mm. The granular pattern formed along weak, curving, semi-diagonal longitudinal grooves on the internal face of the gland has been enhanced by staining with methylene-blue chloride. On this face (at 80x magnification) the epithelium may show islands of unstained clear cells in a field of stained smaller cells. In some snails the whole surface is broken up into large clear polygonal areas, a condition seemingly enhanced, or caused, by effects of dissecting or preservation fluids. In most specimens indications of pores could not be found on this face, despite very close examination. In some cases, with some doubt, there appeared to be many pores. A stratum of dusky granular pigment underlies this face, which appears to be ciliated overall.

FIGURE 13. The bursa copulatrix of 17 specimens. Several populations are represented. Similar variation was found within a single laboratory population. The orientation and relative size of the organ, with respect to the anterior prostate (stippled) is indicated in seven of the drawings. All of the bursas are oriented to indicate how they were found to be postured in relation to the posture of the uterovaginal tract as indicated in Fig. 1. The full length of the bursal stalk is very accurately represented in all cases. The free end of the bursa tends to be differentiated in having a somewhat thickened, densely plicate wall. The outer bursal surface bears fine criss-crossing muscle fibers. The stalk is longitudinally plicate, internally, and generally flattened. The bursa varies from a pale yellow through orange, to brick-red in color, and sperm masses and egg-cells - at least 6 in one case - have been found within it.

Scale as in Fig. 1. Recorded shell-lengths, mm: a, 10.4; g, 9.9. The remainder of the examples represent a somewhat wider range in size.

FIGURE 14. The albumen gland of 24 specimens from several populations. Similar variation occurred in a single laboratory population. The oviducal crook is shown in place in 2 examples. The glands are shown oriented individually to indicate, in comparison with Fig. 1, their discovered posture in relation to the crook. Examples a to h show the same face, usually markedly convex. The others show their opposite face, which is usually weakly concave and nearly flat. Sometimes a portion of the gland, as in c and l, tends to be an almost separate structure that readily breaks away in dissection. Otherwise, the gland tends to be compact and resists fragmentation.

Scale as in Fig. 1. Recorded shell-lengths, mm: b, 9.3; d, 10.4; m, 11.7; o, 10.0. Remaining examples represent a somewhat wider range in shell-size.

FIGURE 15. The prostatic tract. The drawing is based on 2 individuals about 9 mm in shell-length. The example of the tubular posterior prostate, shown with 2 cross-sections, shows its natural curvatures. The narrowing of its posterior 3rd, and the irregularities and general flattening of its remaining part may represent distortions caused by pressures from adjacent organs. Generally the organ is nearly cylindrical and of nearly uniform diameter throughout. For its length it has a thick soft wall of a consistency and color hardly unlike that of the anterior prostate. Only exceedingly delicate, superficial musculoid fibers can be vaguely detected in it in dissection. The vas deferens arises by an abrupt transition as a decidedly muscular, rather capacious tube bearing little, if any, glandular elements. A small indistinct portion of the shown ventral wall of the anterior prostate, where

the vas arises, is somewhat musculomembranous, and may bulge outward. This region evidently underlies a quite small, irregular cavity. z. gr. = zone of pale-blue granules which glow in reflected light in the living organ.

FIGURE 16. The entire male tract, from a snail having a shell 11.7 mm long, drawn to the same scale as Fig. 1. The tract was somewhat stretched while being fixed.

FIGURE 17. The anterior prostate of 18 specimens representing several populations. A cross-section in black silhouette is shown, f. The organ is always rather flat, as indicated. The examples are oriented to indicate their observed orientation, by comparison with Fig. 1. Examples q to s are seen in dorsal view. Organ i is from a specimen completely lacking a penial complex. Scale as in Fig. 1. Recorded shell-lengths, mm: h, 9.9; i, 10.4; l, 9.3; q, 10.6.

FIGURE 18. The penial complex in its natural retracted posture, showing its extrinsic musculature. That musculature is delicate and loosely organized. Aside from the preputial retractor, all of these muscles are interpreted to be tensor-retractors with respect to the preputium. Even the largest ttensor-retractor is not a distinct muscle; it largely consists of separate strands arranged side by side so as to create a somewhat sheet-like structure. That muscle relates to a common tendency for the preputium to be inflated in its middle region. In adults, the vas deferens issues from the body wall in contact, or near-contact, with the preputial base. In progressively smaller specimens, the vas issues, progressively, from points less distant from the female pore. The preputial retractor largely attaches to the penis sheath.

col. mus. = columellar muscle; lat. mm. she. = musculomembranous sheet issuing from the lateral body wall; prepu. = preputial; tensor-retr. pm. = primary tensor-retractor.

FIGURE 19. The penial complex of 9 specimens, representing several populations. Complex i was found everted from the body of the snail. Examples a and e represent live dissections, the others having been preserved. Complex e was fixed while being stretched. Complex g has not been stretched. Some of the variation shown relates to preservation factors and to fixed states of contraction of various elements of the intrinsic musculature. The specimens were all treated with relaxing agents, but the complex reacts variably to such treatment. The bulge in the preputium of h enclosed a mass of sperm. The penis sheath consistently is distinctly spotted externally. Dissecting example a free of the body wall of the snail has allowed it to expand at its base. The vas deferens characteristically narrows distinctly as it joins the sheath. The entire complex is of rather delicate consistency. Scale as in Fig. 1. Recorded shell-lengths, mm: a, 11.0; b, 14.0; c, 14.7; d, 10.3; e, 11.3; f, 10.5; g, 10.6.

FIGURE 20. The penial complex. The penis sheath is spread open in a, and the penis (ultrapenis) has been completely removed from it. The preputiums of 2 specimens, b and c, were longitudinally split open, and are shown spread out to reveal their interior walls. Two sections, b, reveal that the pair of longitudinal "pilasters" are weakly developed. In some examples these structures are yet less well-defined. The overall fold pattern varies considerably from specimen to specimen. Most often there is an evident complex pattern of folds between the pilasters, but sometimes large areas of the preputial wall may be rather smooth.

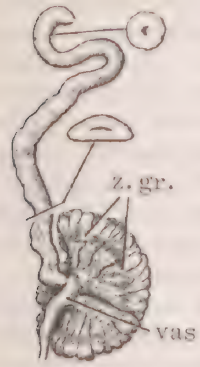
It is thought that such variation largely depends on transiently occurring states of contraction and relaxation of intrinsic and extrinsic musculature. The penis sheath largely consists of circular musculature and it appears to have a thin external longitudinal muscle layer. Along much of the length of the organ, circular elements bounding the cavity of the sheath tend to be split off in ring-like groups by invasions of that haemocoelic cavity among them. Poorly defined circular, or perhaps semicircular or somewhat spiral, delicate and pigmented "festoons" on the wall of the sheath appear to issue from such rings. The festoons seem to be much-split and perforated semi-membranes of connective tissue, partially of cobweb-like appearance. Perhaps they function, hammock-like, in positioning and supporting the convolutions of the penis when it is tucked away in the sheath.

Examples b and c, respectively, are the same as e and g, Fig. 19. fest. = festoons; spl. c. m. = the more pronounced splits in the circular musculature.

FIGURE 21. The ultrapenis of 4 specimens. Example a was dissected from a preserved snail. The other examples were dissected alive in a relaxing fluid. Examples c and d have been stretched, the latter maximally. Preserving fluids of the strength usually used for biological materials may cause marked shrinkage and "condensation" of the tissues. This induces a brittleness and much irregular wrinkling in the penis when it is preserved, complexly folded up in its sheath. Because of fixation of the wrinkles and convolutions, which are impossible to undo, usually little about the structure and intrinsic form of the preserved organ can be determined by dissection. When extracted alive from its sheath in relaxing fluid, the organ straightens out readily and takes on a characteristic shape. This action appears to be due to turgor-pressure created by swelling of a thin mucoid fluid in the penial lumen, but turgescent-appearing hyaline bodies in the penial wall may be involved also. Like a balloon, it has an inherent shape which appears when the proper inflation-pressure is applied. It is difficult to distinguish the epiphallus from the penis proper. Stretching of d has helped demonstrate the division between the 2 parts, by inducing a marked constriction at their juncture. Examples b and c show partial eversion of the penis (the minute portion extending below the given line). No yellow was ever seen in any part of the epiphallus or penis proper. In life the organ is cloudy-whitish-colorless with opaque white areas. It has a vague bilateral symmetry, and examples b to d are shown in side view.

Scale as in Fig. 1. Shell-length of c: 11.0 mm. Specimens a and b are also represented in Fig. 19, b and a respectively, and specimen d is represented in Fig. 16. Examples c and d are shown more enlarged in Fig. 22.

FIGURE 22. The ultrapenis of 2 specimens shown in Fig. 21. The penial bulb contains a mass of tissue which appears to be glandular and partly extra-epithelial, and formed around a complex lumen. Masses of cells of similar appearance surround the epithelial tube in the adjacent portion of the vas deferens. Throughout the epiphallus a superficial stratum of longitudinal muscle-ribbons overlies a stratum of circularly or semispirally oriented muscle ribbons. On the bulb, the longitudinal ribbons tend to be delicate and fused to form a more "conventional" longitudinal layer, but elsewhere the ribbons, both longitudinal and circular, are quite coarse, kinky, well-separated entities. This pattern continues onto the penis proper where the noted features are yet more pronounced. In the terminal 1/3 of the penis proper, the musculature becomes modified to form fine muscle layers of the more conventional type. Hyaline bodies of turgid appearance, and brilliantly white "calciferous concretions," are wedged among the muscle ribbons throughout most of the epiphallus and penis proper. Both types of bodies are more concen-



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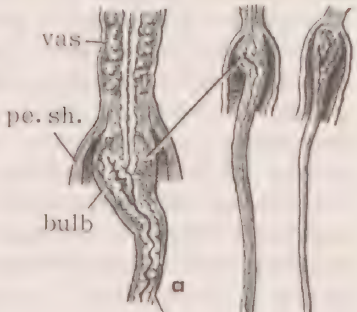

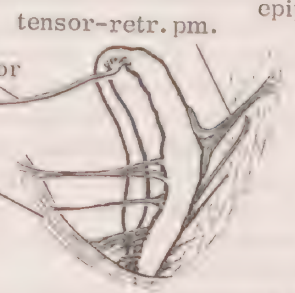

18

posterior prostate

19

21

penis proper

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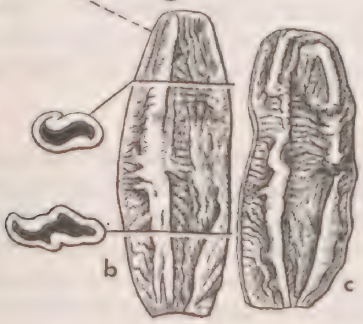

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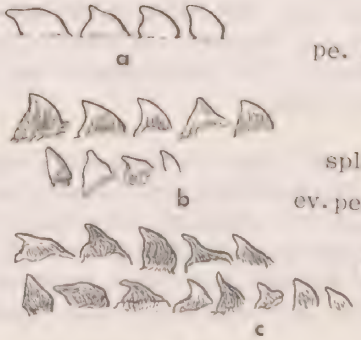

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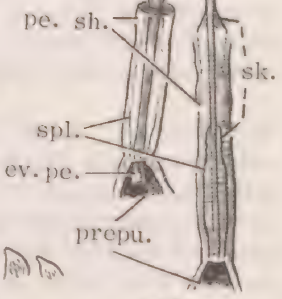

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trated in the epiphallus, especially in its thickest terminal region, which has an especially dense, firm consistency. "Concretions" may be concentrated in the bulb. The epiphallar lumen evidently follows an irregularly spiral course, a condition which is exaggerated when the lumen is largely closed, as often seen in preserved material, by "condensation" or shrinkage of the organ's tissues. When the lumen is expanded, as shown here, the spiral condition is obscure. Long-spiral to nearly circularly oriented, partly close-set epithelial ridges appear to intrude on the lumen also. Accordingly, when the organ is viewed by transmitted light the lumen may appear as a sharply zigzag line as in a, so that the epithelial wall appears coarsely dentate. The ridges, then seen partially in cross-sectional plane-of-focus view, contribute to the dentate appearance as in b. The penis proper may show an even more coarsely zigzag lumen, and an exaggerated pseudo-dentate condition, when preserved in its sheath. Penial tags - somewhat spinelike cuticularized "papillae" - were difficult to demonstrate by dissection. In some specimens they seemed to be largely lacking, although it is believed they were actually present in numbers. The figured number and spacing of the tags is somewhat uncertain. Even the terminal end of the penis - everted in b - appears to bear tags. Tags often appeared to be present in parts of the epiphallus, but their identity could not be confirmed. The shown differences between the 2 ultrapenes largely reflect effects of variations in technique. The series of inflations in the terminal half of b are artifacts.

The terminal fourth of the penis proper is attached to the penis sheath by musculomembranous "skirts" - apparently 3 - which seem to issue from successive, partly overlapping cylinders of circular muscle, arranged like the sections of a telescope. Stretching of the penis (cf. Fig. 21) of both examples caused the more terminal muscle cylinders to telescope more deeply within the base of the sheath, expanding it. This enhanced the constriction separating the juncture of the sheath with the preputium.

ev. pe. = everted portion of penis; pe. sh. = penis sheath; prepu. = preputium; spl. = split between 2 main telescoping circular muscle-groups; sk. = skirtlike connection between the penis and its sheath. Details shown were largely determined by transmitted light at magnifications up to 1000x after the preparations were stained with methylene-blue chloride.

FIGURE 23. Penial tags of the penis proper of a specimen 10.6 mm in shell-length. These are all that could be discerned in an entire organ, dissected alive, mounted whole, compressed under a cover-slip, stained with methylene-blue chloride, and viewed by transmitted light under an oil immersion lens. The structures shown chiefly seem to represent cuticularized portions of the tags. The cuticle tends to take up the stain and the beaks of the tags stain more darkly. While the cuticle seems to form solid tips on the larger tags, it appears to be very flexible, so that the form of the tags might readily be distorted. This may account for the odd shapes. However, several of the more aberrant-appearing shapes, like that of the 2nd largest tag shown, tended to recur in preparations made in the same way.

FIGURE 24. Penial tags of the penis proper. In a, 4 shapes which were seen in uncompressed preparations are illustrated. To an extent, these may represent alterations in posture which an individual tag may undergo, in relation to tensions and pressures exerted by structural elements in the penial wall. It appears that the base of the tags readily undergoes constriction and expansion. For some unclear reason they look more uniform in shape, and thicker and more rounded in contour,

when viewed by reflected light at lower magnifications, after tearing the organ open. Tags of 2 long-preserved specimens are shown in b and c; all that definitely could be discerned by transmitted light in the stained, compressed penis are shown. When so viewed they appear to be flat. The lines shown in them indicate the arrangement of elongate cells having large nucleolated basal nuclei, which make up the tags and support the cuticle. Apparently most or all of the tags are positioned at points where a circular and a longitudinal muscle-ribbon cross in the penial wall. At such points the 2 ribbons seem to interconnect by 1 or several muscle fibers, and to send some fibers into the base of the tag. Indications of this condition appear in b. To an extent, then, the muscle-ribbon system seems to be an anastomosing network.

Scale approximately as in Fig. 23. The specimens represented in b and c, are represented, respectively, in Fig. 19, d, and in Fig. 21, a. Specimen c is also represented in Fig. 19, b.

PART II.

Liberian *Bulinus* (*Physopsis*) *globosus* (Morelet). Reproductive anatomy. (Exception: Fig. 3). The data given here was derived from a large part of several thousand specimens, collected or reared by the author and representing 45 field populations. Refer to the introduction to Part I for information relating to the following figures. This species probably should be synonomized with *B. africanus* (Krauss, 1848), and be known by that prior name.

FIGURE 25. A representative shell of *Bulinus globosus*. It has 4 3/8 whorls and is from a field population. The shell of the largest specimen found was 17.1 mm long, and had 4 5/8+ whorls. Morphological sexual maturity is attained generally by the time the shell reaches 8 mm in length. Individuals as small as 7.6 and 7.8 mm in shell-length were seen to mate, respectively, as a male, and as a female.

FIGURE 26. The reproductive system, egg capsule, and (in dashed outline) the egg mass. The drawing is based on nearly 1000 dissections, and observations on hundreds of egg masses. The reproductive system as a whole is notably deficient in dark pigmentation, and has a "clean" look.

FIGURE 27. A "pericardial organ" of a type discovered in *Bulinus globosus*. This example is from a *B.* (*Physopsis*) *nasutus* from Tanzania. *B. forskalii* and *B. truncatus* have a comparable organ, but that of the latter is a diffuse, far-less-well-defined structure.

ky. = kidney; ol. vnt. = outlet of the ventricle of the heart, which has been removed; pcd. = pericardium or pericardial; q. se. or. = a questionable anatomical entity, that might be a secondary pericardial organ.

FIGURE 28. Relationship of the postoviduct to the uterovaginal tract, partly indicated by a generalized "curving cross-section." Note the muscle fibers binding the oviduct to the uterus.

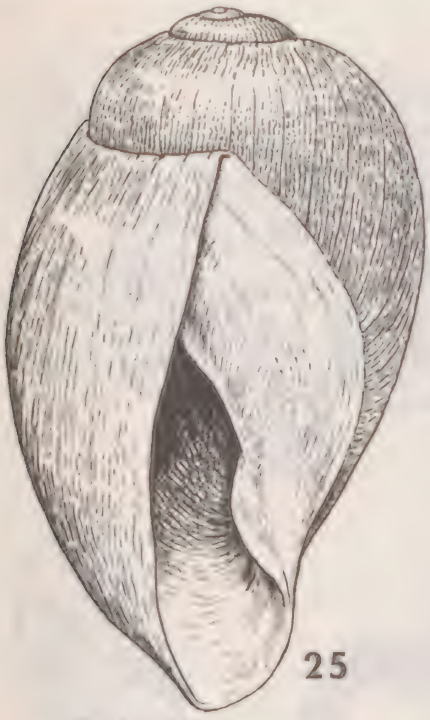
FIGURE 29. The carrefour complex, with arrows indicating the theoretical pathway of the oocyte as it becomes inseminated, embedded in "albumen," and passes into the prooviduct. oo. indicates approach of the oocyte toward the carrefour.

FIGURE 30. The ovotestis of a selected specimen. The same individual is represented in Figs. 31, 32 and in c, Fig. 34. Numbers identify acinus-clusters correspondingly numbered in those figures. The gonad is relatively free of blackish pigment and has a clean appearance. a. c. = anterior collecting (canal); gran. bl. = orange-brown granular blotches; p. c. = posterior collecting (canal); y. = bright yellow.

FIGURE 31. Structural analysis of the individual gonad shown in Figs. 30 and 32. Given are a diagram, a, of the exact disposition of the acinus clusters; a precise scale-drawing, b, showing the shape of the collecting canals and the disposition of the outlets of the acinus-clusters; and a cross-sectional view, c, of the gonad. A reticulate whitish pattern which may form on the inner walls of the acini in under-preserved specimens is indicated in c.

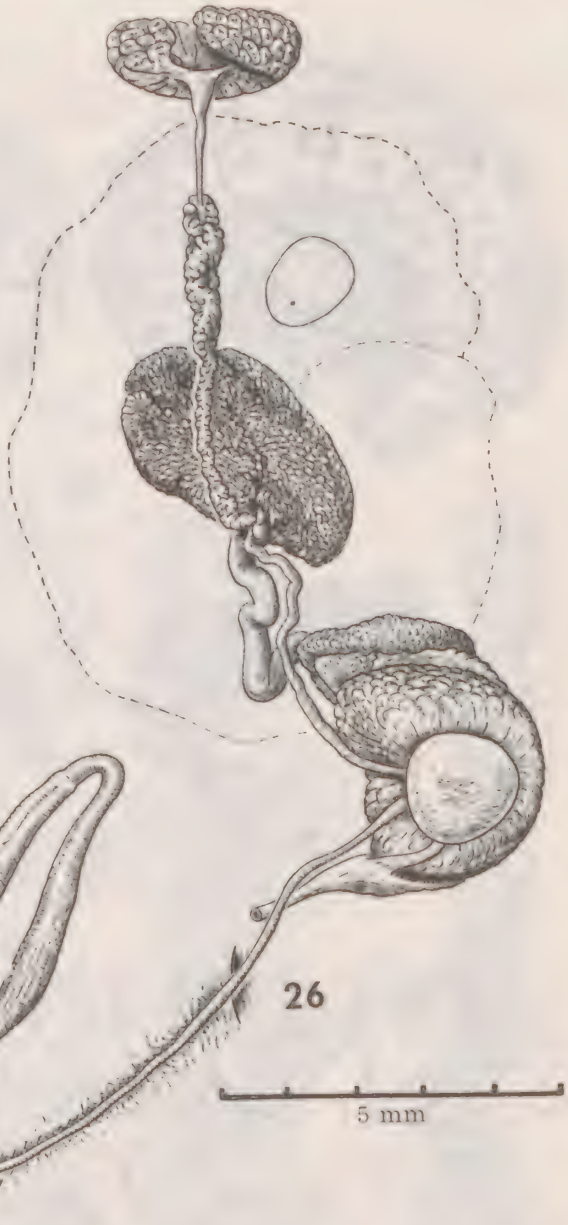
FIGURE 32. All of the acinus-clusters of the gonad shown in Figs. 30 and 31. The anterior collecting canal appears in cross-section in cluster 6. The scale applies with somewhat varying exactitude to the individual clusters.

FIGURE 33. Analysis of the gonad of a specimen having a shell 9.3 mm long.



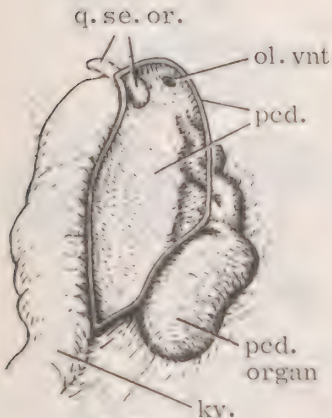
25

5 mm



26

5 mm



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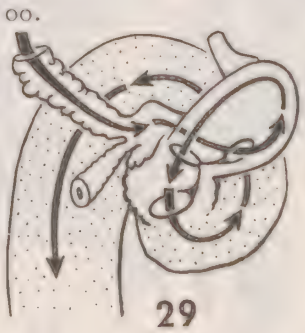
28



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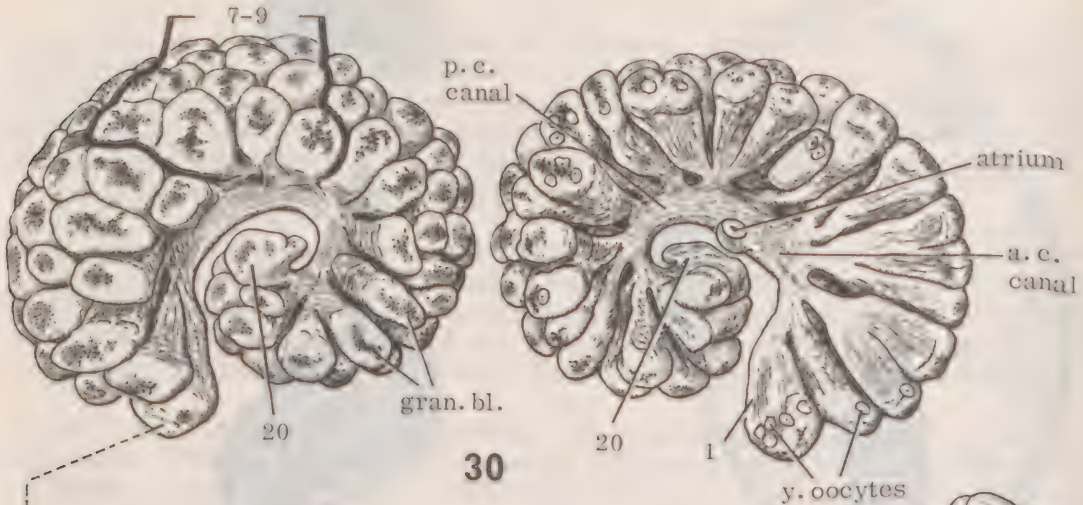
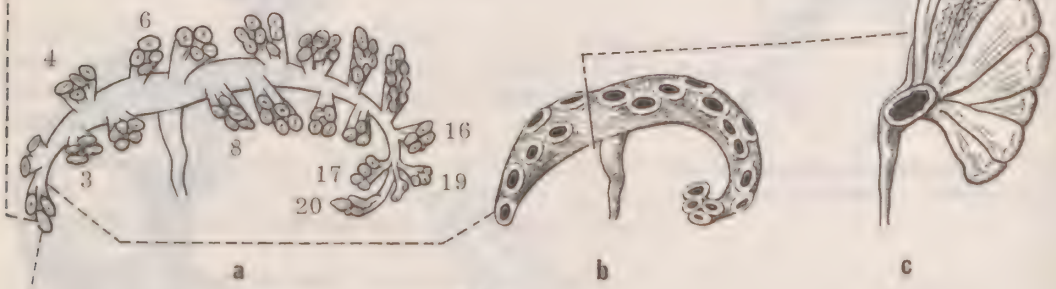

7-9
p. c. canal
atrium
a. c. canal
gran. bl.
20
20
1
y. oocytes

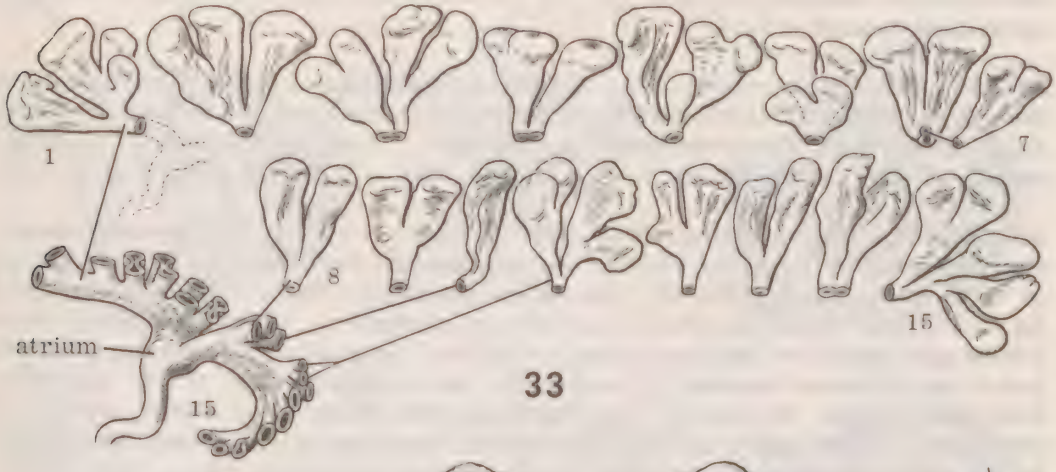
30


6
4
8
16
3
17
19
20
a
b
c

31

1
2
6
7
10
11
15
16
17
20

32



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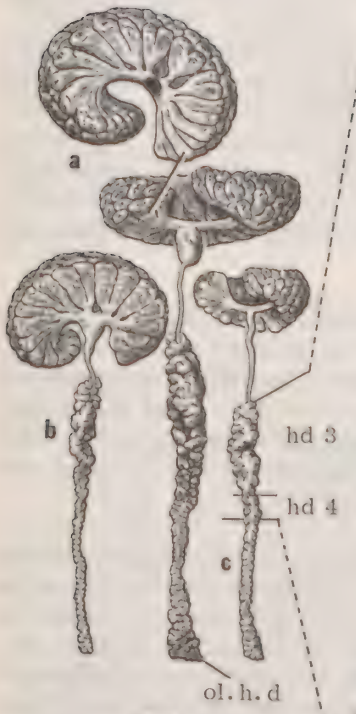

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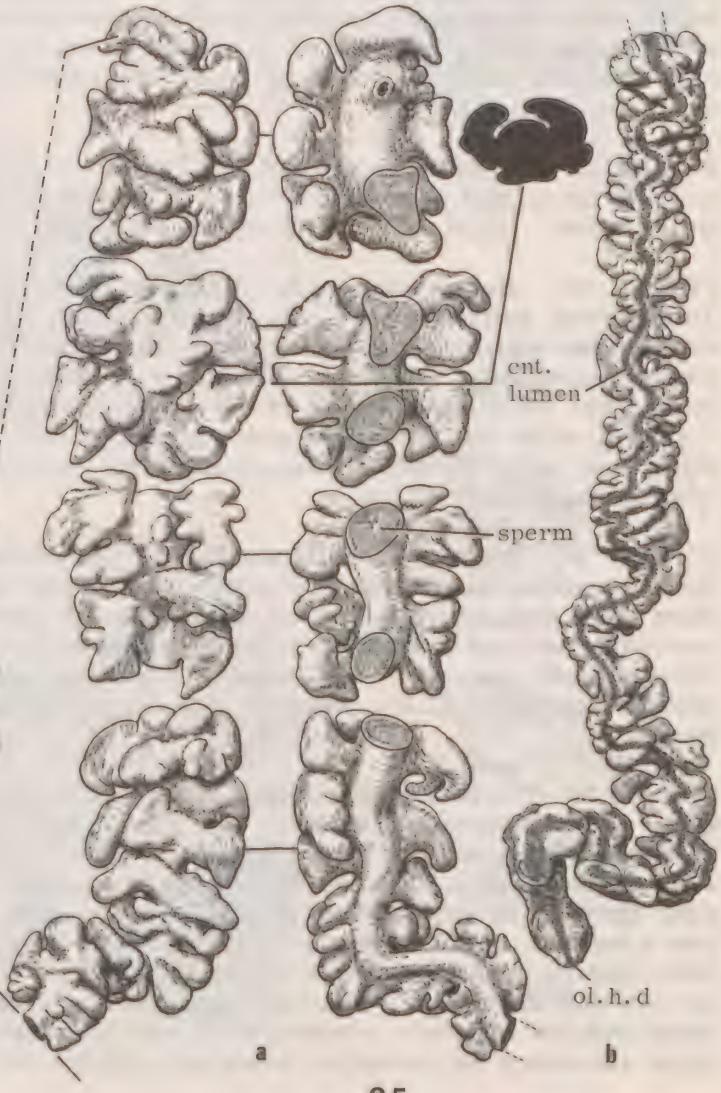


35

Scale for the clusters as in Fig. 32. The atrium-collecting canal system exhibits a presumably postural variant.

FIGURE 34. The hermaphroditic system of 3 specimens. Example c represents the same specimen as do Figs. 30-32 & 35. In the separated view, gonad a has been flattened. Scale as in Fig. 1. Recorded shell-lengths, mm: a , 15.2; c, 15.0. ol. h. d. = outlet of the hermaphroditic duct; hd3, hd4 = divisions 3 and 4 of the duct.

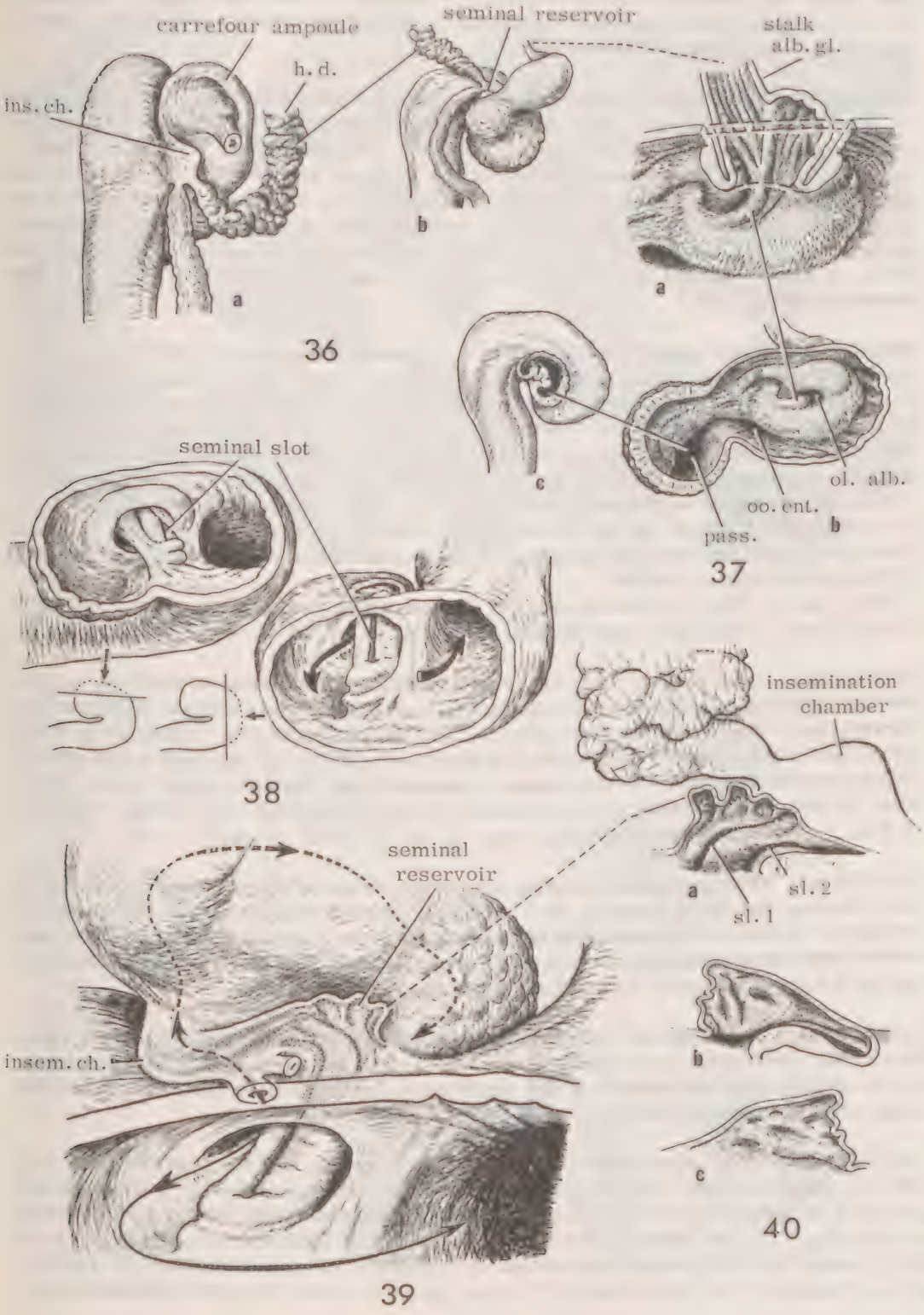
FIGURE 35. The hermaphroditic duct of example c, Fig. 34, showing features characteristic of Liberian snails. To demonstrate the details in a, the tract had to be untwisted very tediously, and cut into sections. The indefinite division 4 of the tract in a connects directly to that in b, division 5, which naturally is much folded upon itself, but which has been unravelled. Its projecting vesicles, pustules, and kinks are bound together by a webwork of musculoconnective fibers, eliminated here (cf. a, Figs. 36 and 40). This division looks much wider than it actually is, especially near its outlet, until it is unravelled. Stippling in b indicates the primary lumen, which communicates with cavities in the vesicles and pustules. The swelling at the outlet appears to be thickly muscular but may not be a definitive structure. Note that the inlet into division 3 is subterminal in position. cnt. = central: ol. h. d. = outlet of the duct.

FIGURE 36. The carrefour complex. The ampoule is shown in its usually observed posture, in a, and twisted aside in b. The hemispherical glandular passage is quite yellow. h. d. = hermaphroditic duct; ins. ch. = insemination chamber.

FIGURE 37. Internal structure of the carrefour ampoule and adjacent parts. The internal surfaces shown are heavily ciliated, especially the almost shaggy elevated pad surrounding the outlet of the stalk of the albumen gland. The hemispherical passage's wall is composed of very large, high-columnar translucent cells. The exact configuration of the outlet region in c is slightly conjectural. alb. gl. = (of the) albumen gland; ol. alb. = outlet of the stalk of the albumen gland; oo. ent. = the oocyte's entranceway into the ampoule; pass. = passageway leading into the oviducal crook.

FIGURE 38. Views of internal surfaces of the oviducal crook showing the oviducal columella from 2 different angles, in the same specimen. In the columella there is a conspicuously ciliated, very deep slot and a secondary deep groove. Arrows in the tract indicate the presumptive mode of entry and exit of the freshly "albuminated" egg-cell - the forming capsule - into and from the crook. The crook's inner surfaces are generally ciliated, and its wall is actually thicker than figured.

FIGURE 39. The relationship among carrefour structures at the oviducal columella. The insemination chamber has been folded somewhat downward and the hermaphroditic duct and posterior prostate have been cut away to expose the seminal reservoir. The arrowed line beginning in the hermaphroditic duct indicates the path the oocyte would take as it is inseminated and becomes incorporated into a capsule. Stippling represents conspicuous ciliation having a golden reflectivity that is visible externally in the indicated pattern. The seminal reservoir is very delicate and very difficult to demonstrate by dissection. The slot clearly leads into the reservoir, which clearly leads into the insemination chamber, but there are minor complications which are not perfectly clear. No seminal gutter


carrefour ampoule
h. d.
ins. ch.
a
seminal reservoir
b
stalk
alb. gl.
a
36
c
ol. alb.
oo. ent.
b
pass.
37
seminal slot
38
insemination
chamber
a
sl. 2
sl. 1
seminal
reservoir
insem. ch.
39
b
c
40

was identified elsewhere in the oviduct. It seems odd that the seminal pathway in the oviducal columella arises so abruptly without continuity with such a gutter. insem. ch. = insemination chamber.

FIGURE 40. The seminal reservoir. Example a shows 1 internal wall and 2 slots on either side of an extension of a major fold of the oviducal columella. These slots' relationship to the seminal slot is not perfectly clear. Slot 1 (sl. 1) evidently leads from the deepest portion of the seminal slot. Slot 2 (sl. 2) leads into the insemination chamber. Another example, in b, presents the same wall and illustrates a postural variant. In it the 2 slots appear to be identifiable but closely juxtaposed. The opposite wall of this example is revealed in c. The internal walls of the organ are so densely ciliated that the pockets and crevices in it look decidedly fringed.

FIGURE 41. The albumen gland of 18 specimens, representing about 10 populations. The organs are arranged to indicate their observed individual orientation in respect to the prooviduct (cf. Figs. 14, 26). The organ tends to be brittle and relatively loosely organized. In dissection it often fragments readily. To some extent the cracks shown are artifacts. The vermiform nature of its component tubules is relatively obvious on its surface. The organ is not very thick, and commonly its edges tend to be rolled inward so that it appears narrower and more compact than it really is, as in example b, where the gland in one view has been "unrolled" and flattened out somewhat. Most of the other examples also have been flattened out to some extent.

Scale as in Fig. 1. Shell-lengths of the specimens ranged from about 8 mm to about 15 mm. Recorded shell-lengths, mm: d, 13; j, 15.2; l, 13.3; o, 15.0.

FIGURE 42. The oviduct of 5 specimens, and the postoviduct of another, representing several populations. Examples a and b show their natural postures and curvatures; the others are more or less straightened out. Example e, while alive, was exposed to alcohol while being stretched, and in the process some minute bulbous pustules formed on its surface. Example f has been dissected apart somewhat to demonstrate that it is composed of many glandular diverticula. Scale as in Fig. 1. Recorded shell-lengths, mm: a, 13; d, 15.2; e, ca. 9; f, 12.

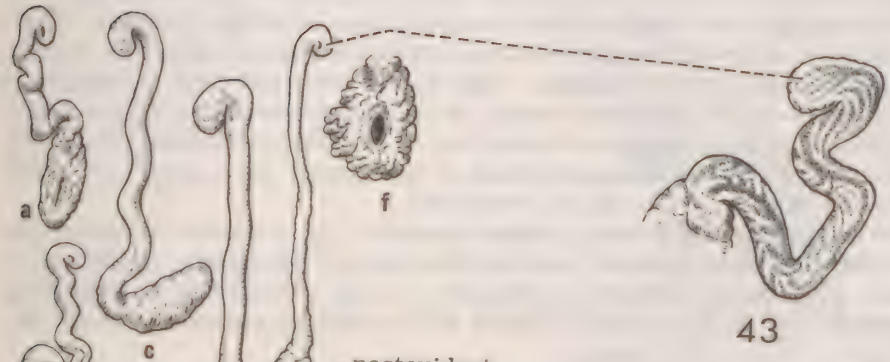
FIGURE 43. The prooviduct, showing the natural bends of the particular specimen, and showing the main aspects of a complex pattern of glandular folds (stippled) formed on its inner wall. Outwardly the tract is relatively smooth, yet shows a very fine, dense pustulation associated with the larger folds. The shown face of the blind end of the crook is more distinctly, though finely, pustulate.

FIGURE 44. The external and internal structure of the postoviduct, and its relation to the prooviduct, in a selected specimen. The organ is massively glandular. In the shown detached portion of the prooviduct a diverticulum has been dissected away from its normal position. ol. = outlet.

FIGURE 45. The uterovaginal tract of 9 specimens, and the uterine gland of 2 others, representing several populations. For examples h and i, the anterior prostate is indicated in dotted outline. Examples a and b were fixed while mating as females. In the former, the penis is just barely inserted in the vagina. In b, the greater part of the penis is coiled up within the bursa copulatrix (cf. Fig. 61, c), surmounted by a white mass of sperm (sp.). A brown, swirled, diffuse, semi-

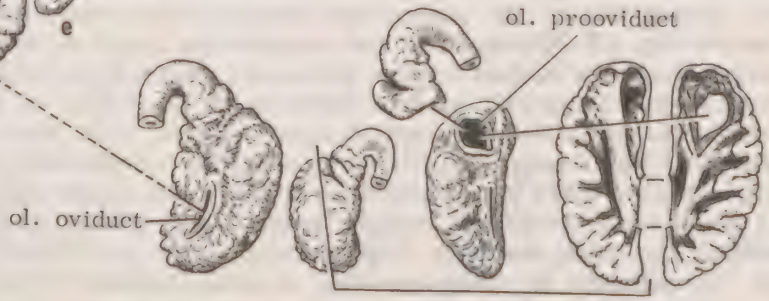
a
b
d
f
g
h
i
j
k
l
m
o
p
q
r

41


a
b
c
d
e
f

42

43


postoviduct
ol. proovidu ct
ol. oviduct

44

liquid matter surmounts the sperm-mass, as a polar cap. Example f was dissected alive in a relaxing fluid, and as it eventually began to deteriorate it was treated with alcohol; as a result, it shows effects of both swelling and shrinkage. The variation among the other examples is interpreted as being largely postural. The ventral division of the uterine gland tends to be separate from that gland, and may be poorly developed and obscured by fibrous tissue. The bursa of f, h, and i has been pulled out of its natural position.

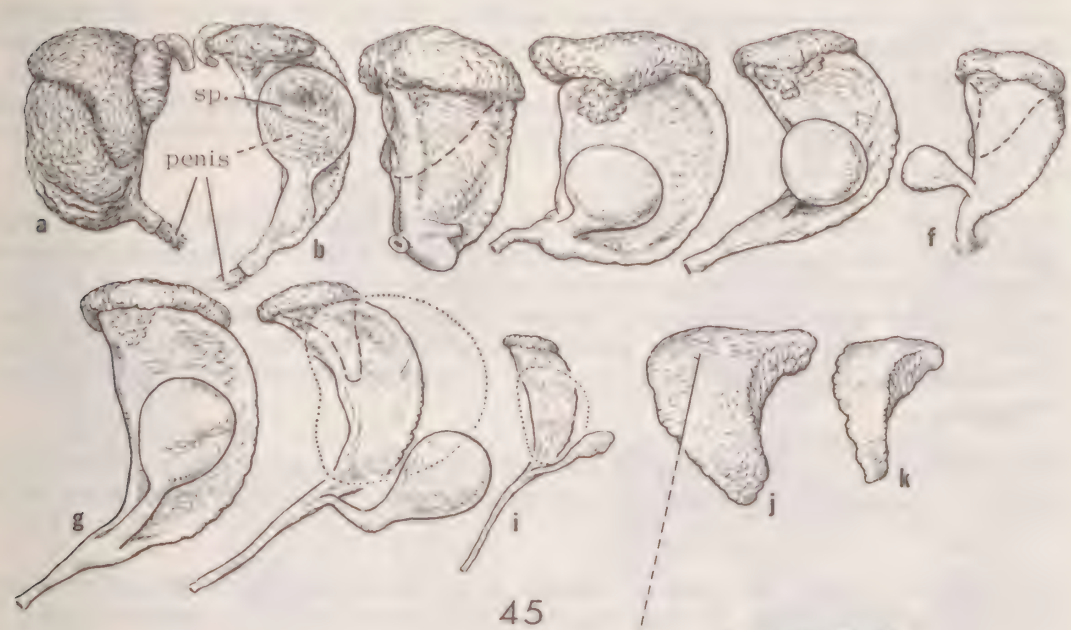
Scale as in Fig. 1. Recorded shell-lengths, mm: b, 13.0; d, 12; e, ca. 13; f, ca. 9; g, 13.3; j,12; k, 13. The other specimens fell within this range of size.

FIGURE 46. The uterine gland of a specimen having a shell-length of 14.8 mm. On the gland's inward face, in this and many specimens, pores could not be detected; instead, an areolate pattern was in evidence. In others, areolae were not developed and minute pores of irregular size and spacing seemed to occur. The areolae appear to be patches of swollen cells in a field of more normal-appearing epithelial cells. In some specimens the areolae were larger, separated by little intervening space, and of a more definite, irregularly polygonal shape. Such variation may relate in part to effects of preserving and dissecting fluids. When areolae are underdeveloped, the whole internal face of the gland is found to be ciliated; otherwise, cilia seem to be limited to the inter-areolar spaces. In color, the gland ranges from buff to somewhat red-brown, and is practically free of dark granular pigment.

FIGURE 47. The uterovaginal tract. The drawings represent an analysis of characters of many specimens, and shows details especially drawn from a specimen having a shell 15.2 mm long. A "resting" posture is indicated. Views b and c show the internal walls of the tract, which are well-ciliated throughout, as around the outlet of the stalk of the bursa. The uterine gland in c shows a granular pattern brought out by staining. The uterine folds generally are bevelled-carinate. What is termed the seminal gutter is broadly continuous with the space called the uterine vestibule, into which the oviduct opens. The yellow external field is composed of massed, flattened-down pustules whose cavities communicate by pore-like openings with fold-fissures that are extensions of the uterine lumen. The post-oviduct lies outward to the vestibular pocket of the uterus. In b, pore-outlets of the ventral division of the uterine gland are visible.

d. f. g. = fold delimiting the seminal gutter dorsally; do. = dorsal extension (of the); i. f. = internal fold-fissure marking the edge of the uterine gland; ol. = outlet (of the); y. = bright yellow structures; v. f. g. = ventral fold delimiting the seminal gutter; v. s. g. = space forming the ventral extension of the gutter.

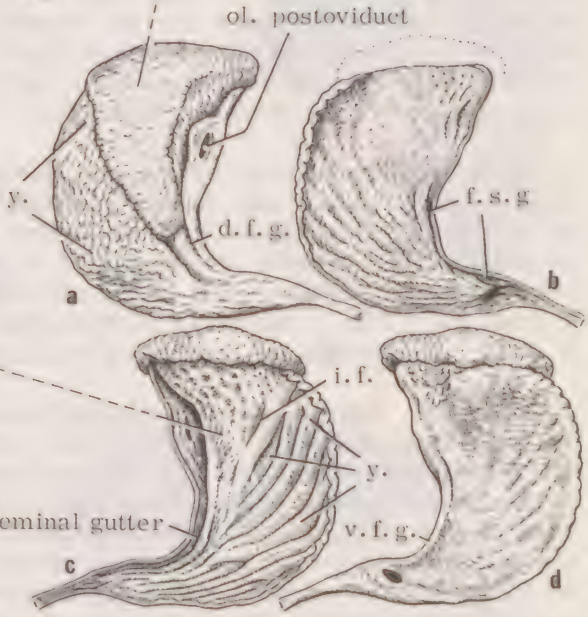
FIGURE 48. The bursa copulatrix of 17 specimens, representing about 10 populations. Orientation of the organs with respect to the uterovaginal tract is indicated as for Fig. 13. The position and shape of the anterior prostates of 3 specimens are indicated in dashed outline. Example c shows a yellow pustule, evidently containing a wasted egg-cell, as does the bursa shown in Fig. 45, i. This condition was seen in similarly small bursae of similar shape, in *B. forskalii* and *B. truncatus* (cf. Fig.78,s). Example d is shown in side view, illustrating the way the stalk generally attaches more or less dorsally to the bursa. Internally, the attachment area is glandularly thickened, radially plicate, and coarsely ciliated. The stalk is generally flattened, inwardly longitudinally plicate as indicated in g and l, and ciliated. In example m, criss-crossing musculoid fibers on the bursa are indicated. The contents of the organ vary in color from white, through shades of


sp.
penis
a
b
f
g
i
j
k

45

internal
fissure

46


ol. postoviduct
y.
d. f. g.
f. s. g
a
b
i. f.
y.
do. seminal gutter
v. f. g.
c
d

47

dorsal
a
d

e
f
q

48

yellow and orange to wine-red, and may include a brown to purple-blackish material marking the upper pole of the mass. The bursa and the stalk regularly are rather thin-walled.

Scale as in Fig. 1. Shell-lengths of the specimens range from about 8 to 15 mm. Recorded shell-lengths, mm: e, 15.2; k, 14.8. Examples of more bursae are shown in Fig. 45, to the same scale.

FIGURE 49. The male reproductive system of a specimen having a shell about 9 mm long. The tract was fixed while being stretched out. The region of juncture between the penis sheath and preputium has been especially stretched, and the circular muscle-masses there have "popped" into the sheath's base in a telescoping action. The penis sheath of the specimen is shorter than that of most specimens. Scale as in Fig. 1. ju. = juncture; tel. c. m. = bulge containing telescoped circular muscle.

FIGURE 50. The prostatic tract of a selected specimen, with cross-sections of the posterior prostate, the *in situ* contortions of which are illustrated. Scale as in Fig. 1.

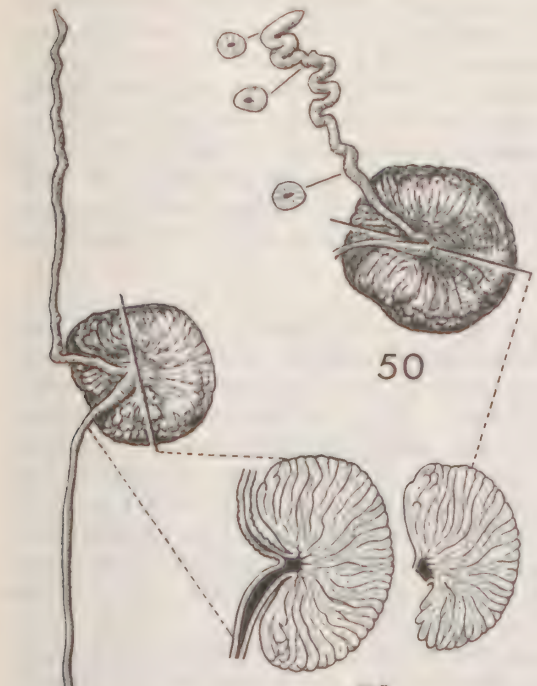
FIGURE 51. Shape and internal structure of the anterior prostate, as revealed by 2 transections made at right angles to each other. The individual clusters of branched glandular tubules are not clearly discernable in dissection, and cannot be teased apart, so the pattern shown is slightly generalized. The tip of each tubule contains a few coarse white granules; in combination, these create a thick "cortical" pseudostratum of whiter appearance.

FIGURE 52. The anterior prostate of 12 specimens representing several populations. Orientation of the organs is indicated as in Fig. 17. Example l is shown in dorsal view, the others in ventral view. The portion of the posterior prostate crossing to the organ's atrium generally is embedded in a groove in the organ's surface, usually within a well-developed sheath of connective tissue.

Scale as in Fig. 1. Recorded shell-lengths, mm: a, 15.2; b, 13.3; c, 12; f, 13; l, ca. 9. Shell-length for the series ranges down to about 8 mm.

FIGURE 53. Internal structure of the penis sheath and preputium of a specimen 13.3 mm in shell-length. The sheath has not been stretched. The same specimen is represented in Fig. 55, b. The many curved transverse lines in the narrow part of the sheath indicate abundant split-off edges of circular muscle groups. Above, a relatively strongly developed longitudinal muscle layer on the external wall of the sheath shows through weak circular musculature from which the festoons appear to be partially developed. The edges of some festoons appear to be reinforced by a thin band of muscle. The arrow indicates the direction of viewing into the sheath permitted by a cut made where indicated.

FIGURE 54. The natural posture and extrinsic musculature of the penial complex, as found in a specimen with a shell 11.5 mm long. The preputial retractor, although it functions as such, is largely inserted on the penis sheath. Other intrinsic muscle fibers are arranged around that insertion so as to maintain a sharp flexure in the basal region of the sheath. Although rather coarse, none of the retractor-tensors of the preputium are well-defined muscles; they consist largely of separate strands. The vas is usually in contact or near-contact with the preputial base. Scale for the whole complex as in Fig. 1.



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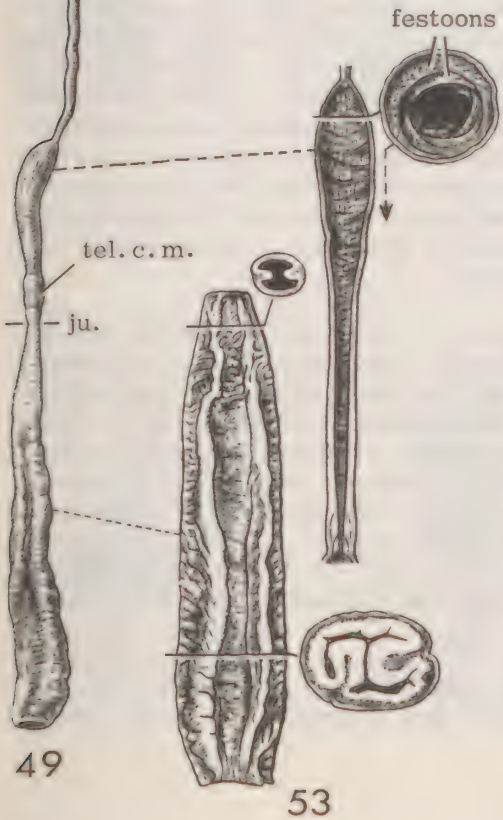
51

52



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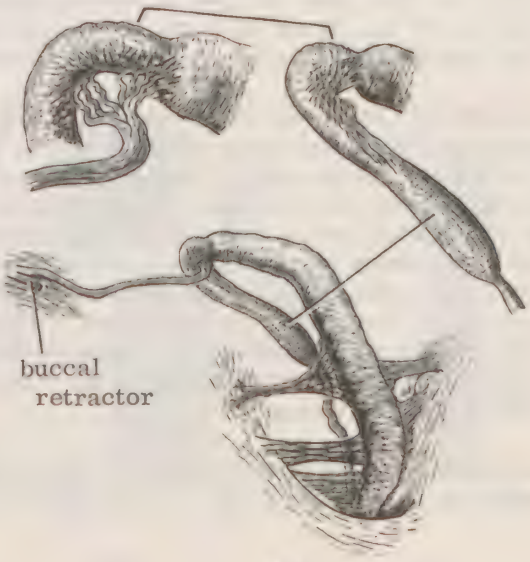

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FIGURE 55. The penial complex of 5 specimens representing several populations. The dotted outline connected with example a indicates the extent to which the preserved preputium could be stretched. Examples c and d are also preserved. The latter evidently shows shrinkage, as apparently did the ultrapenis in it, which was partly everted and looked much slenderer than that of other specimens. Examples d and e represent live dissections. Examples b and e show the anterior face of the preputium and indications of the well-developed pilaster internal to it. The longitudinal surface musculature of the sheath appears to be somewhat split and shredded longitudinally, and is transversely wrinkled. Scale as in Fig. 1. Recorded shell-lengths, mm: a, 15.2; b, 13.3; d, 9.2; e, 8.3.

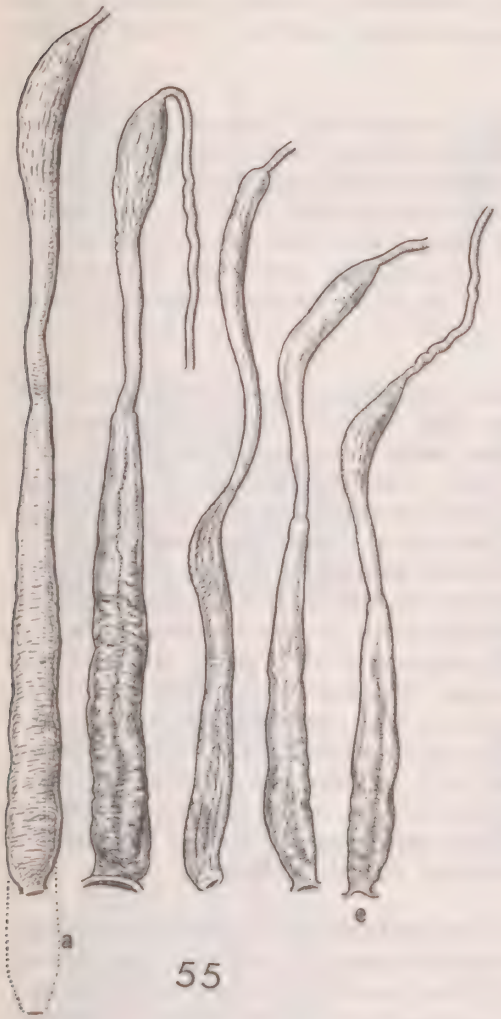
FIGURE 56. Details of structures at the apex of the penis sheath, in 2 specimens, a and b, partly revealed by 2 cross-sections of the vas and by longitudinal cuts through portions of the sheath and the epiphallus of the ultrapenis, and partly demonstrated by transmitted light and staining. In a, the size of the epiphallar bulb relative to the thickness of the sheath's wall, and to the haemocoelic cavity of the sheath is especially indicated. In that specimen the bulb was attenuated by stretching and was demonstrated to have a surface layer of longitudinal muscle, which gives rise in the succeeding narrow part of the epiphallus to separated longitudinal muscle-ribbons. The bulb contains a seemingly glandular convoluted mass which appears to be continuous with similar tissue in the vas, and with the thick epithelium of the succeeding part of the epiphallus.

c. m. = circular muscle in the section of the epiphallus, apparently circularly oriented muscle-ribbons; gl. = (apparently) glandular; l. m. = longitudinal muscle in the epiphallus, actually longitudinal ribbons.

FIGURE 57. The ultrapenis of 4 specimens. Example a was extracted from a preserved specimen; it was exceedingly wrinkled and contorted, and was straightened out to the degree shown only with much difficulty. Little could be determined of its form and structure. Example b was extracted alive in a relaxing fluid and fixed while being stretched maximally. Before stretching, it much resembled example c. Specimens c and d were extracted alive in relaxing fluid and allowed to take on their intrinsic form. The living ultrapenis was always seen to be largely or entirely colorless-bluish, grading to mottled-cloudy-whitish, but it often showed yellow in the apex of the penis proper and in a short region of the epiphallus adjacent to it. Scale as in Fig. 1. Shell-length of specimen c, about 9 mm. The other specimens were adults of unrecorded size.

FIGURE 58. Structure of the wall of the retracted penis proper and of the adjacent portion of the epiphallus, of specimen c, Fig. 57. The coarseness of the ribbons is slightly exaggerated. In the region of the section "calciferous concretions" are so densely concentrated that they greatly obscure the illustrated details. When the epiphallus tissues are condensed by preservative, many hyaline bodies project markedly from the surface as if extruded by pressure. Except in the bulb, the entire epiphallus is structured as in the shown part. The cross-section seems to show tags like those in the penis proper; these perhaps are only cut-through ridges. The epithelium in this region is often yellow (y.). Although not so figured, hyaline bodies, positioned much as shown for the epiphallus, occur throughout most of the penis proper.

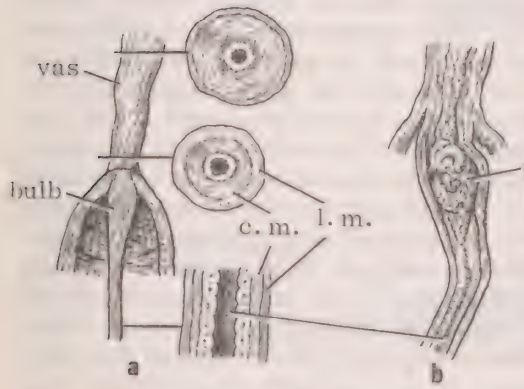
FIGURE 59. The relationship of the basal region of the penis proper to musculature at the juncture (ju.) of the penis sheath and preputium. Circular muscle


a
e

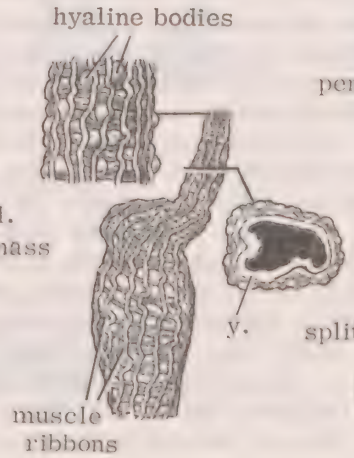
55

epiphallar
bulb
a
d

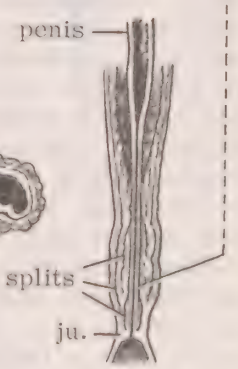
57


vas
bulb
c. m.
l. m.
a
gl.
mass
b

56


hyaline bodies
y.
muscle
ribbons

58


penis
splits
ju.

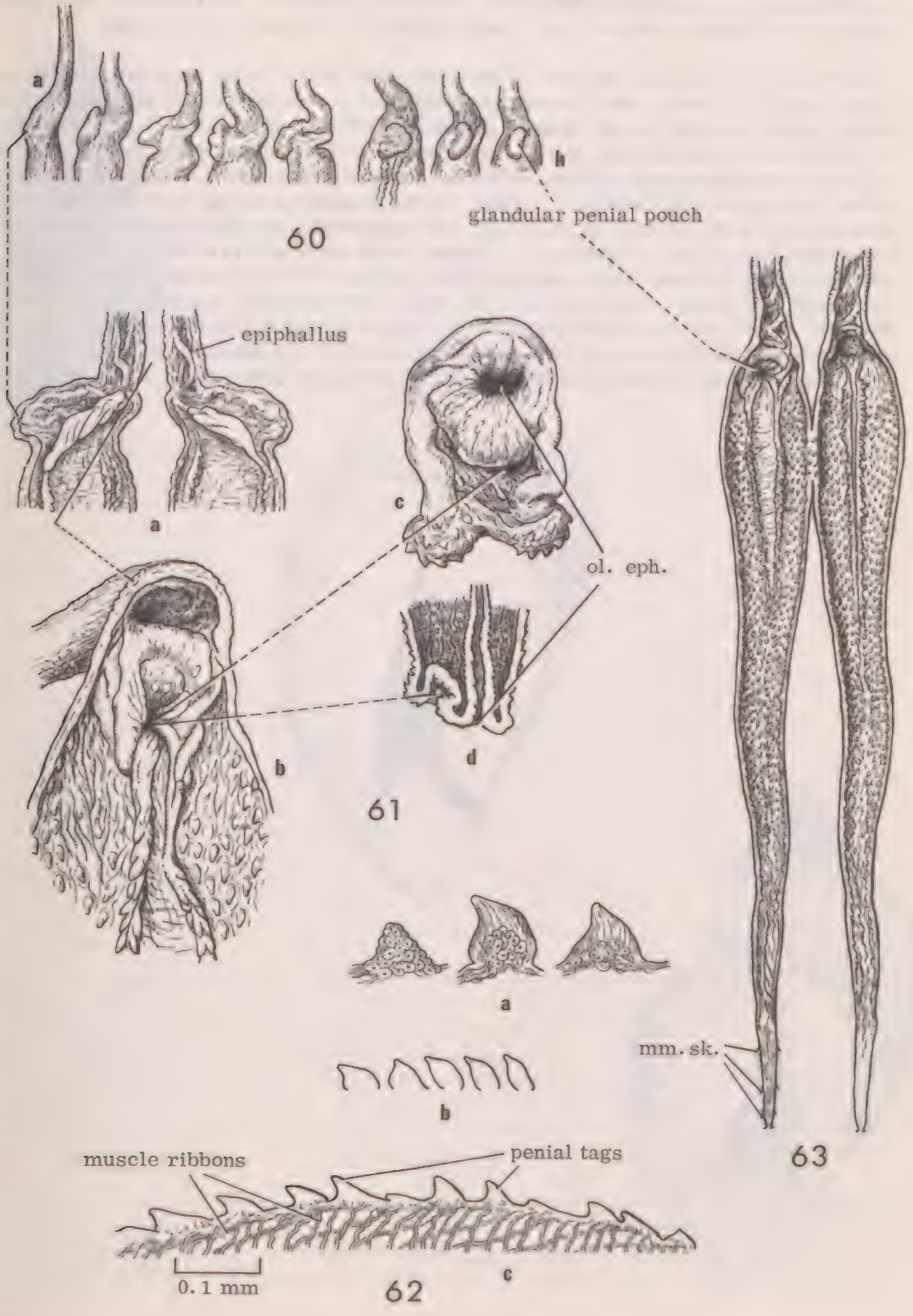
59

groups, separated by splits and skirt-like membranes within the bulge in the sheath, have been telescoped into that region by tension applied in stretching the penis in dissection (cf. Fig. 22, especially c).

FIGURE 60. The glandular penial pouch of 8 specimens, from several populations, as seen on the outer surface of the retracted ultrapenis. Example a is the same as b of Fig. 57, in which the ultrapenis has been stretched while alive. When dissected, examples b to d had been preserved a short time in a relatively weak preservative, and largely had retained their natural form and color. The others were dissected alive. Examples a to e are seen in side view. The variation in shape evidently is largely postural. Often the pouch is wholly or partly yellow. Recorded shell-lengths, mm: b, 13.5; c, 11; e, 15.7; f, ca. 10; g, 13.5.

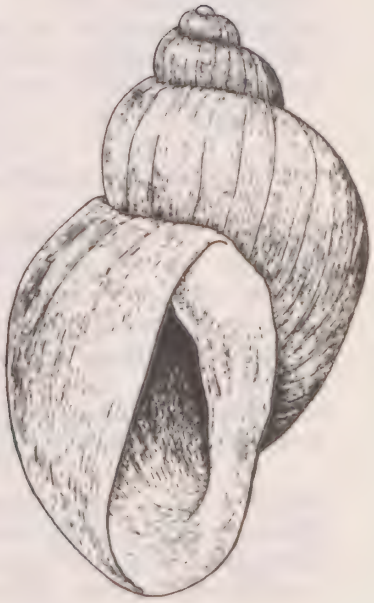
FIGURE 61. Structures of the apical region of the penis proper, including those that form the definitive end of the organ when fully everted. Details enhanced by staining, seen by transmitted light in a live preparation in relaxing fluid, are revealed in a in opposite side views of the region. The internal wall of the pouch is so thickened by a complex of glandular folds, that details of it in such views are beclouded. In b, the region in a live specimen is cut open to reveal the outlet of the pouch and its associated fold-complex. In this specimen various components of the complex are suffused or bordered with yellow, especially bright where the folds issue from the pouch. The color extends onto 1 or more ridges spiraling into the epiphallus, and onto the non-papillate portions of the 2 pairs of long folds extending toward the opposite end of the penis. Example c presents an end-on view of the functional end of a fully everted penis. It was dissected from the copulatory bursa of acting female b, Fig. 45. Structures revealed by a longitudinal cut through the end of that penis are represented in d, slightly generalized. Incomplete correlation among minor details of structure seen in the different views is to be noted. Example a is the same as c of Fig. 57, and is shown in Fig. 58. Shell-length of specimen b: 14.3 mm. ol. eph. = outlet of the epiphallus.

FIGURE 62. Penial tags. Tags as seen by transmitted light in the fresh penis proper in the retracted state, stained and mounted under a cover slip, are shown in a. In one adult snail the tags on the whole looked much as in the first drawing, like a pile of large nucleolated cell-nuclei bearing no evident cuticle. Similar ones occurred here and there in examples having generally more typical tags that evidently represent a more mature development. The other drawings in a show repeatedly seen shapes which seem mostly to represent postural variation. The fibers crowded into the base of the tags are muscle strands which evidently arise from the penial muscle ribbons. Shown in b is the apparent variation in form of tags within a single penis, and in specimens generally, as seen by reflected light on cutting the retracted organ open. For some reason the most elongate forms, like the last 3 shown, were never seen when using transmitted light. The tags glisten by reflected light, especially the longer, more cylindrical ones with pronounced beaks. In some specimens such reflectivity was detected with difficulty or not at all, and the tags may have a fleshy appearance on the whole. The tags tend to be opaque white, and generally, each is centered on a diffuse oval "halo" enclosing scattered subepithelial "calciferous concretions" that also tend to crowd into the bases of the tags. Tags as seen in silhouette on an everted penis proper are shown in c, along with a representation of the general arrangement of the penial muscle ribbons. On the several everted organs studied none of the tags appeared to be sharply beaked, narrowly cylindrical, or basally constricted. The


a
h
60
glandular penial pouch
epiphallus
a
c
ol. eph.
b
d
61
a
b
mm. sk.
63
muscle ribbons
penial tags
0.1 mm
c
62

everted penis is filled with red blood. The scale applies to the tags in c very precisely, to b roughly, and not to a. Shell-length of specimen b: 15.2 mm.

FIGURE 63. The penis proper in the retracted living state, inflated in relaxing fluid, and split open and folded outwardly to reveal its inward surfaces. The details were mostly drawn from a specimen having a shell about 8 mm long, but in snails up to the largest sizes, no differences were noted, except that the tags in larger specimens may appear to be even more abundant, more cuticularized and more crowded than indicated. Tags on the 2 pairs of elongate folds tend to be arranged in 2 or 3 series on each fold, and apparently are fleshier and less cuticularized than those elsewhere. These folds were always seen to be entirely whitish except in their initial non-papillate portions, the 4 of which may be yellow, especially in larger specimens. The tags are decidedly arranged in curving-diagonal rows in a cancellate pattern. Sometimes tags seemed to be almost certainly present in the very end of the penis attaching in the base of the penis sheath, but sometimes they could not be definitely identified there. mm. sk. = skirtlike membranes.



PART III.

Egyptian *Bulinus* (*Bulinus*) *truncatus* (Audouin). Reproductive Anatomy.

Note: Much of what would be essentially a repetition of that described in Parts I and II is left aside here. See the explanatory remarks preceeding Part I, in which information on scales applicable to the following figures is given. The figures on this species are based on many hundreds of preparations made from laboratory populations maintained in Liberia from 1959 to 1961, and which had derived from a single strain cultured for many years previously by Hans Vogel at The Tropeninstitut, Hamburg, Germany. The field locality in Egypt from which the strain originated is unknown to me.

FIGURE 64. A shell of about maximum size of the strain studied. It has 4 1/2 whorls. Most members of the strain had shorter, blunter spires. The snails generally attained morphological sexual maturity on reaching a shell-length of about 8 mm.

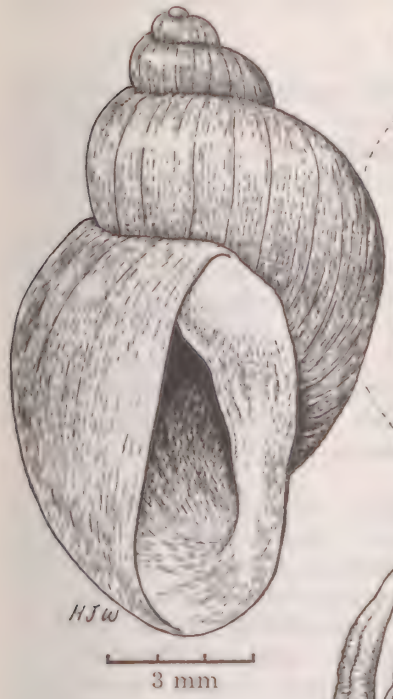
FIGURE 65. The entire reproductive system, with an egg mass indicated in dashed outline as enclosing an egg capsule. The anatomical drawing, as a summation and extract of results pictorially presented afterward, indicates what may be considered the most nearly typical expression of characteristics observed in the species, and the egg mass is represented on a similar basis. The posterior prostate might be taken as somewhat exaggerated in respect to its length, but perhaps it is able to stretch to that extent in life. The system, on the whole, exhibits considerable granular dusky pigmentation. The thick egg mass has a conspicuous internal fibro-lamellar structure.

FIGURE 66. The hermaphroditic system of 8 specimens, shown whole or in part. Examples of the ovotestis d, e, f and h, are flattened out and somewhat distorted as a result. Division 1 of the hermaphroditic duct of example h is swollen by matter from the ovotestis forced into it during flattening of the latter. The entire hermaphroditic duct is shown in examples e to h. Only e, f and h represent living preparations. Approximate surface counts of acini of c and d, respectively, were 35 and 45. In 2 unfigured specimens ranging up to 12.1 mm in shell-length, about 37 acini were counted in one, and 48 in the other.

Scale as in Figs. 1 and 65 (etc.). Shell-lengths of the specimens, mm: a, 10.0; b, 11.1; c, 10.0; d, 12.8; e, 10.2; f, 9.4; g, 10.0; h, ca. 9. Specimens a, b, and h are also represented, respectively, in Figs. 67, 68, and 69.

FIGURE 67. The ovotestis of specimen a, Fig. 66. This example has about 18 acini in its adapical division and about 12 in its anterior division. The apices of its acini are suffused with orange-red instead of being distinctly blotched. Definite blotching occurred in other specimens, but not very commonly. The relative smallness of the oocytes indicated here might be characteristic of the studied strain, but this was not confirmed. The example has a definite, short posterior collecting canal, but no definable anterior one. 1 = an acinus of the most abapical cluster. A cross section is given to the upper right.

FIGURE 68. Morphological analysis of gonad b, Fig. 66. The adapical face is represented in a, where the organ is shown separated into its posterior and anterior divisions. Acini of a given cluster are shown separated only by stippled areas, and the clusters by black areas. The length of the posterior collecting canal is



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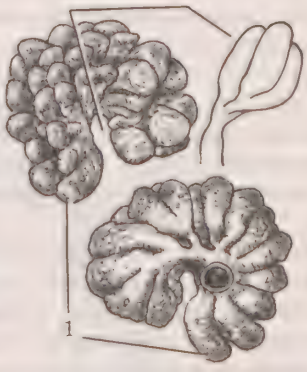
66



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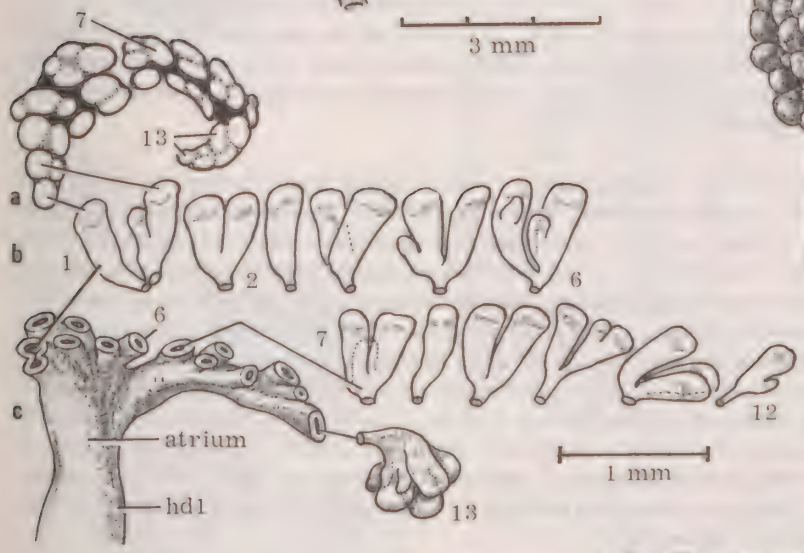

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69

slightly exaggerated in c. The scale applies to a and b; c is more enlarged. hd1 = 1st division of the hermaphroditic duct.

FIGURE 69. Analysis of gonad h, Fig. 66. Collecting canals and the anterior and posterior gonadal divisions were not clearly definable in this example, and the sequential positions of the acini were only arbitrarily definable in part. This condition probably reflects a postural state. Scale as in Fig. 68, for the acini.

FIGURE 70. The hermaphroditic duct of specimen e, Fig. 66. The vesicles in division 3 have been spread to the sides of the tract. They are all stubby, and extend but slightly over the smooth rachis visible in the drawing to the left. Division 5 is ill-defined and not definitely folded upon itself. Its enlarged appearance is mainly due to a concentration of pustules and swollen wrinkles on it. The small vesicle shown on division 2 is not a constant feature. Very little variation from the indicated characters was noted in other specimens. hd1 to hd5 = divisions 1 to 5 of the duct. A cross section in silhouette is given.

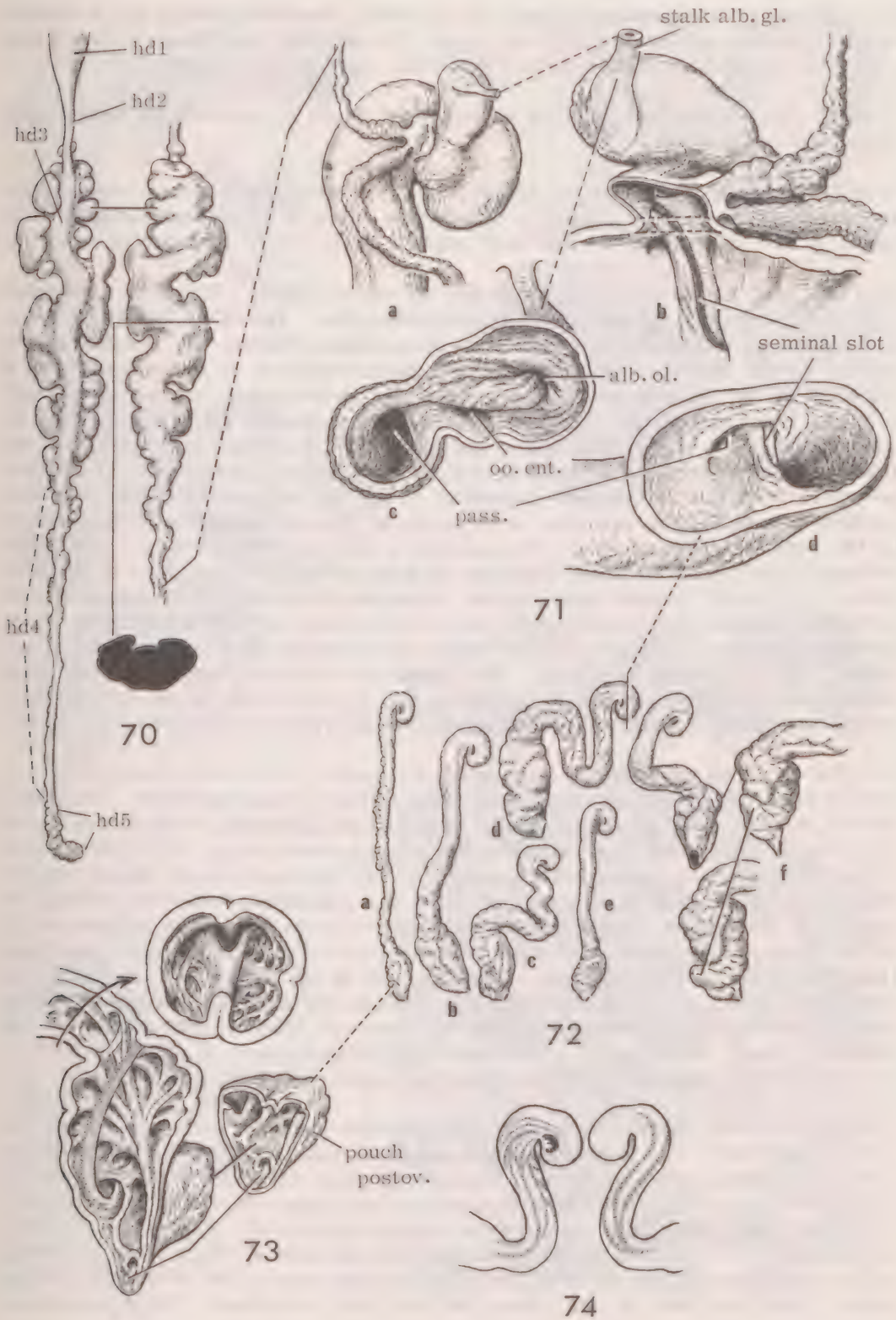
FIGURE 71. The carrefour complex. The carrefour ampoule has been raised and twisted to the right in a to reveal the insemination chamber and the seminal reservoir. The reservoir appears to be smooth and non-digitate, but its exact form was not ascertained. Only 1 cleft was found in the oviducal columella - the heavily ciliated seminal slot. The large, densely ciliated fold issuing from the outlet of the stalk of the albumen gland is diagonally plicate. Whether such relatively minor features were constant in the studied strain was not established. The oviducal crook, however, constantly is notably smooth externally, on all sides. Drawing b is partially a reconstruction in which the relationship of the seminal reservoir to the seminal slot may not be quite perfectly indicated.

alb. gl. = (of the) albumen gland; alb. ol. = outlet of the stalk of the albumen gland; oo. ent. = passage by which the freshly inseminated oocyte would enter the ampoule; pass. = cavity leading from the ampoule through the hemispherical glandular passage into the oviducal crook.

FIGURE 72. The oviduct of 6 specimens. Example a was preserved in alcohol while being stretched. In the process, many prominent pustulae formed along its length. Examples b and e are unpreserved and have been straightened out. Example f - shown in 3 drawings - is a fresh preparation, in which the natural curvatures and surface topography of the prooviduct have been modified by swelling of the tract in a dissecting fluid. Its prooviduct is more smoothly contoured than is normal. The remaining examples are preserved and show their natural curvatures, and the enhancement of surface irregularities corresponding to internal folds and associated cavities. Usually the 1/2 or 1/3 of the prooviduct joining to the postoviduct is enlarged. In all cases the oviducal outlet is at the very end of the postoviduct. Of the many glandular pockets making up the latter structure, one is an especially large and distinctive entity. This postoviducal pouch is shown partially dissected free in example f.

Scale as in Fig. 1. Recorded shell-lengths, mm: a, 10.2; b, 12.8; e, ca. 9. The other specimens fell within the same approximate range of size.

FIGURE 73. Internal structure of postoviduct f, Fig. 72, and of the adjacent portion of its prooviduct. The arrow indicates where a cut has allowed looking into the prooviduct in the adapical direction. The details are slightly generalized. The tissues have been macerated to some extent, and the thick glandular linings of


hd1
hd2
hd3
hd4
hd5
70
stalk alb. gl.
a
b
seminal slot
alb. ol.
oo. ent.
pass.
c
d
71
a
b
c
d
e
f
72
pouch
postov.
73
74

the folds and concavities has largely sloughed off. The lining tissue had a spongy-porous appearance, especially in the pouch. The stippled band represents a major fold on the nearer wall that has been removed. postov. = postoviduct.

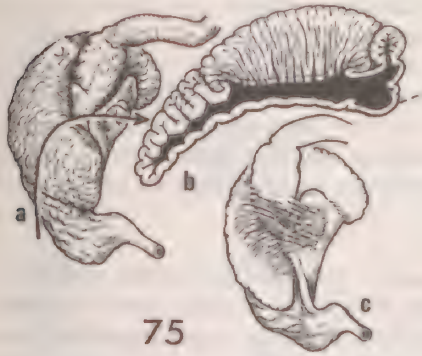
FIGURE 74. Major aspects of the fold-pattern within the prooviduct, indicated by stippling.

FIGURE 75. Relationship of the postoviduct to the uterovaginal tract. The muscle strands binding the postoviduct to the uterine gland are especially coarse. The outlet of the oviduct is at the very edge of the pocket of the uterine vestibule.

FIGURE 76. The uterovaginal tract and the uterine gland. The separated gland, d, is that of a particular specimen of unrecorded size. The other drawings represent features judged to be representative of the strain studied. An external groove related to the seminal gutter is slightly exaggerated in a. A sharp small fold, at the edge of the oviducal outlet, and visible in c, is traceable into the postoviduct. In all of many specimens examined, at least some uterine pores were relatively conspicuous. In some, the entire inward wall of the gland showed closely-set gaping pores of uniform size, yet larger than the largest shown here. Each pore seems to have the independent capability of closing or opening widely. The discovered coarsely fibro-lamellar structuring of the egg-mass doubtlessly relates to the size of these pores. The pores are always surrounded by a pale, often elevated halo, while abundant blackish pigment under the pored face of the gland forms a reticular pattern among them. When the pores gape the pigment is concentrated, so that that pattern consists of conspicuous narrow black lines. It can then be seen that each pore is the outlet of a hexagonally columnar tube of pale tissue having a blackish sheath. The vestibular inflation tends to be somewhat larger and more dimpled in larger specimens. gr. = groove (exaggerated); gu. = dorsal extension of the seminal gutter; y. = bright yellow structures.

FIGURE 77. The uterovaginal tract of 5 specimens. Examples a and b were dissected from preserved specimens; the others were dissected alive. Example c shrank in an alcoholic solution, which enhanced its pustulate condition and that of its bursa. Example d also shows some effects of shrinkage. Example e shows some effects of swelling in relaxing fluid, and the widening of its vagina resulted when that organ was dissected free from the supporting body wall, as was the case with example c. The bursa of a was very thin-walled. Only 1 dissection of an *in copula* acting female was made, and the end of its partner's penis was found inserted in the uterine vestibule. Then the wall of the uterus was found to be infused with blood, the bursa was reduced in size, and oocytes were present in the hermaphroditic duct. Perhaps the bursa does not function in copulation in this species. Scale as in Fig. 1. Recorded shell-lengths, mm: a, 12.8; d, 10.2; e, 10.0. The other specimens fell into the same approximate range of size.

FIGURE 78. The bursa of 19 specimens. Example a shrank while being dissected alive in alcohol. The others are presumably normal; most were dissected from preserved specimens, the others from living ones. Orientation of the organs is indicated as for Fig. 13. With high constancy the bursa showed densely crowded pustules on its base or on the adjacent portion of its stalk. The pustules tend to be arranged in clusters of cauliflower-like appearance, or in rosettes. Also, on the whole, the organs pictured, including smaller ones, have decidedly thickish walls, from one end to the other, and generally are finely rugose-granular-


a
b
c

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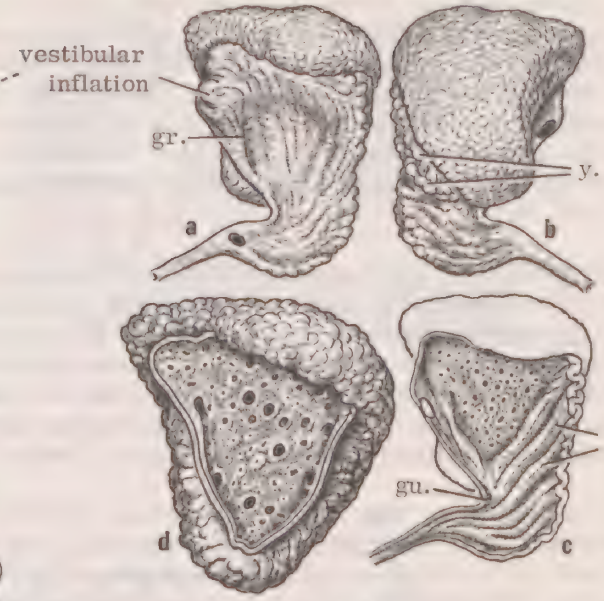
vestibular inflation
gr.
y.
gu.
a
b
c
d

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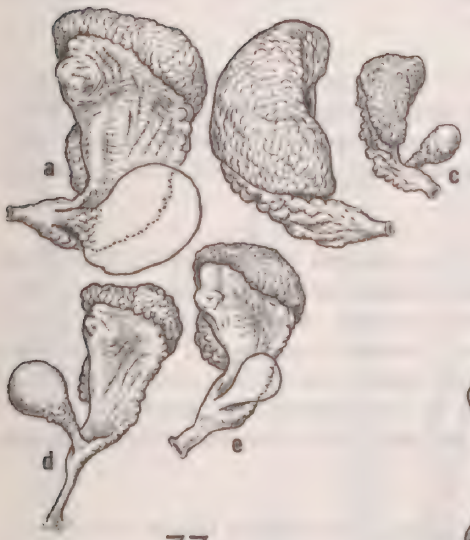
a
c
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a
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v
z
zz
y

79

pustules
a
e
f
j
k
p
q
s

78

plicate over a large part of their external surface. There are several large fold-fissures within the stalk in more typical examples, and the pitlike outlets of the pustules open into them. The entire stalk is shown for all of the specimens. Perhaps the generally observed limited size of the bursa and the thickness of its wall is indicative of the possible infrequency of its use as a copulatory organ. The anterior prostate is indicated in dashed outline for examples q to s. Scale as in Fig. 1. The specimens represented ranged from small-adult to large-adult size.

FIGURE 79. The albumen gland of 27 specimens. Orientation of the organs is indicated as in Fig. 14. The organ tends to be relatively soft, pliable, and resistant to fragmentation. In many instances it is difficult to identify any particular face or end as a topographic feature. Example d is darkly dusky, as are examples u to zz: these evidently are atrophied or are in a physiologically regressed condition. Scale as in Fig. 1. Recorded shell-lengths, mm: b, 12.8; c, ca. 9; d, 10.2. The other specimens fell within this range of sizes.

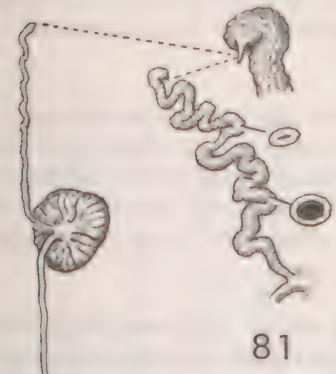
FIGURE 80. The male reproductive system of a specimen about 9 mm in shell-length. The tract has been stretched to some extent, especially around the juncture (ju.) of the penis sheath and preputium, where circular muscle groups (tel. c. m.) consequently have telescoped into the base of the sheath, and have produced a bulge there.

FIGURE 81. The posterior prostate, showing the natural bends and the variation in thickness of the particular example, dissected from a preserved specimen. The organ is relatively delicate, and not very thick-walled. In the immediate region of the larger cross-section it is somewhat brittle and translucent, but otherwise it is soft and opaque-whitish throughout. Each specimen differs somewhat from the pictured details. This example appeared to originate at the hermaphroditic duct by a short narrow stalk, a structure not definitely demonstrated in other specimens.

FIGURE 82. The anterior prostate of 16 specimens. The organ tends to be relatively soft and pliable. Orientation of the organs is indicated as in Fig. 17. Examples o and p present their dorsal faces: the others, their ventral faces. A section, in black silhouette, is represented. The organ was never seen to be very thick. Scale as in Fig. 1. Recorded shell-lengths, mm: a, 12.8; m, ca. 9; o, 10.2; p, 9.4. The other specimens fell within this range of size.

FIGURE 83. The penial complex of 10 specimens. Example a is stretched like the example in Fig. 80. The others have been straightened out, more or less, but not stretched. Festoons on the inner wall of the penis sheath are heavily pigmented and darkly show through that wall. Examples i and j entirely lack a penis, and a dark mass of connective tissue shows through their sheaths. Example a contains a penis having an abnormally short epiphallus, shown in Fig. 86, a. Example h contains a normal penis. Examples a, c, d, e and g represent live dissections in which the dissecting fluid had a slight swelling effect on the contained penis. In fresh specimens, generally, the orange to yellow colors of the penis show through the sheath rather brightly. Commonly the lower anterior border of the preputium is irregularly outpocketed. Scale as in Fig. 1. Recorded shell-lengths, mm: a, 10.2; b, 12.8; c, 9.9; d, ca. 8; f, 12.8; g, 7. The other specimens fell within the same range of size.

FIGURE 84. The extrinsic musculature and the typical retracted posture of the



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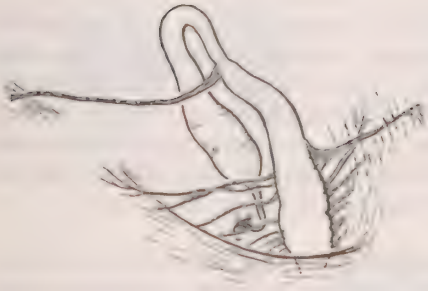

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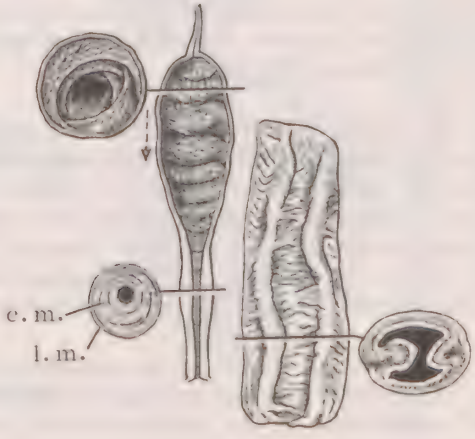

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penial complex. The preputial retractor attaches to the preputium and not to the penis sheath. The vas issues from the body wall relatively far from the base of the preputium.

FIGURE 85. Internal details of the penis sheath, with the ultrapenis removed, and of the preputium. The festoons are especially well-developed, and appear to have their free borders reinforced by a muscular thickening. The arrow indicates the direction of sighting into the interior of the sheath through the transverse cut end of that organ. This example is the same as c, Fig. 83. c. m. = circular muscle; l. m. = longitudinal muscle.

FIGURE 86. The ultrapenis of 5 specimens, in side view. All were dissected out alive in a relaxing solution. Example a has an abnormally short epiphallus; its penis proper is unusually thick-walled and failed to expand normally in the relaxant. The specimen's gonad and albumen gland were abnormally small and dark. Example b has been stretched maximally, with the result that its ribbon-musculature has become densely concentrated and smoothed out. Examples c to e were allowed to relax and take on their intrinsic inflated form. In them, for the most part, the location of each penial tag was clearly marked externally by a whitish to yellowish oval, well-spaced from the others. The adult ultrapenis for nearly its whole length apparently always is more or less orange to orange-yellow in color, and the apex of the penis proper and the adjoining thick and strongly tapered region of the epiphallus are decidedly so colored, with a chalky appearance. The color, at least in part, is in the glandular epithelium. Penis c shows a small everted part which appears to bear tags. Scale as in Fig. 1. Recorded shell-lengths, mm: a, 10.2; b, ca. 9; c, 8; e, 11.9. The other snails fell within the same size-range.

FIGURE 87. Penial tags as seen within the retracted penis proper. Examples a and b show characters enhanced by staining and seen by transmitted light. Example a seems to represent a maturely developed tag and it exhibits a commonly observed form. It probably is not flat, as it may seem to be. Example b evidently represents an earlier stage of development of a tag, not commonly seen in adults. The nuclei are grouped in a hemispherical to conical configuration. The common apparent shape of mature tags, as seen by reflected light, is represented by c. It is shown seated upon a characteristic "halo," wherein "calciferous concretions" and some yellow tissue tend to be concentrated. The apparent relation of the tags to the network of muscle ribbons is indicated in d, but perhaps the arrangement is really not quite so regular.

FIGURE 88. Penial tags in outline, as seen by transmitted light in a retracted penis proper, extracted from a live adult specimen, stained with methylene-blue chloride, and compressed under a cover-slip. The structures shown usually stained well, and stained intensely on their beaks; they apparently represent only cuticularized portions of the tags. Evidently the beaks are somewhat brittle and in some of the shown tags, the tips seem to have been broken off. Flexibility of the remaining cuticle seems to account for other apparent distortions.

FIGURE 89. Relationship of the epiphallar bulb to the vas deferens and penis sheath. The relative capaciousness of the sheath, and the relative delicacy of its walls in comparison to the dimensions of the bulb, are illustrated in example a. This example shows an especially elongate postural attenuation of the bulb. Example b shows the apparently glandular mass in the bulb, as seen by transmitted

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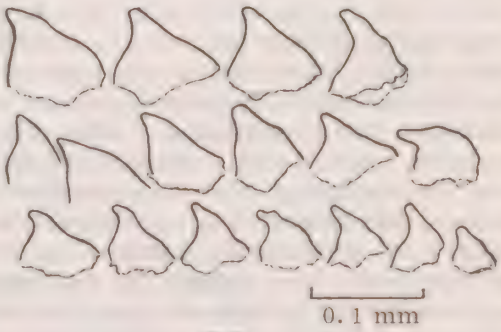

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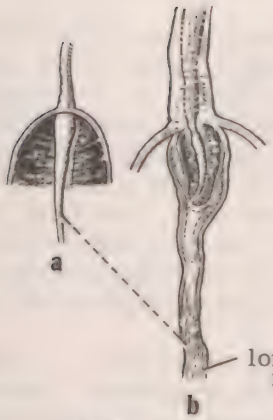
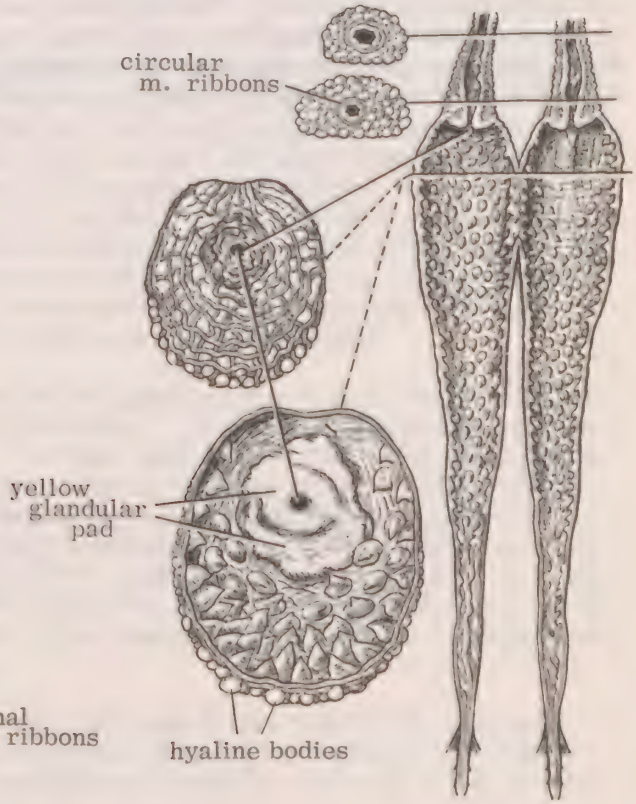


longitudinal
muscle ribbons

89



light after staining. In this instance, the mass appeared to be a compact structure largely unattached to the wall of the bulb, and seemingly unconnected with the epithelium of the following part of the epiphallus; it was easily dissected out. It even appeared to be lined outwardly by an epithelium. Transections made of the shown portion of the vas were essentially identical to those shown in Fig. 56. Note that the end of the vas is expanded.

FIGURE 90. The penis proper in the retractive, inflated state, and the adjacent part of the epiphallus, cut open. Two thick sections of the epiphallus are shown. In that region, that organ's walls consist of a solidly dense mass of "calciferous concretions," yellowish cells, and large hyaline bodies, among which the kinky longitudinal muscle-ribbons are embedded, more or less superficially. A direct view of the inner face of the apex of the penis proper, as permitted by cutting through that organ transversely where indicated, reveals a yellow pad, apparently glandular and non-ciliated. The pad however, unlike most gland-structures, resisted staining with methylene-blue chloride. The yellow tissue extends well into the epiphallar base as an epithelial lining. A comparable view of the apex of the penis proper, less magnified, and as seen by transmitted light, reveals the pattern of musculature outward to the epithelium of the pad and of the region peripheral to it. Within the pad, many fine extensions of the muscle-ribbons anastomose irregularly to form a largely concentric, but very raggedly wavy pattern. On what may be taken arbitrarily as the "front" side of the bilaterally symmetrical penis proper, there is a large area free of tags and having a weak median crease. In less well-expanded examples, the tags are densely crowded and more sharply projecting. The relatively large size of the tags in this species is immediately apparent on opening of the organ. In adults, especially of large size, the tags glisten markedly by reflected light, and obviously appear to be heavily cuticularized. hy. bd. = hyaline bodies of turgid appearance; m = muscle.

PART IV.

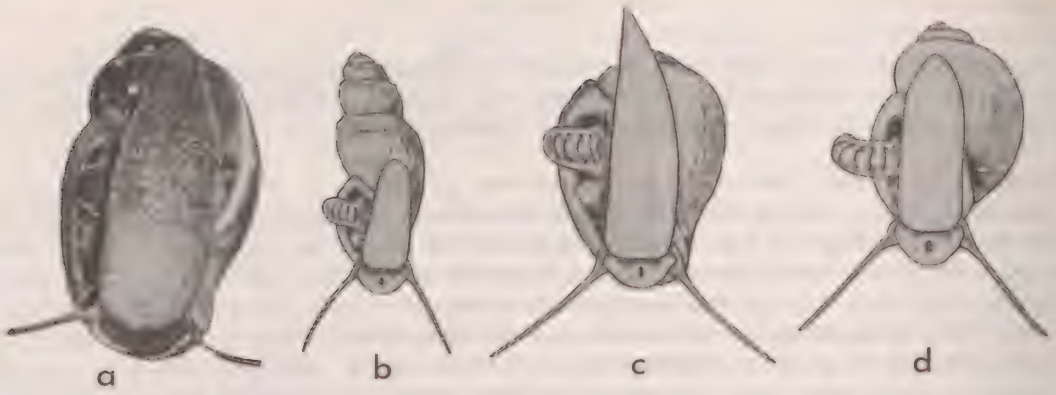
Morphology of the body, teeth, and shell. Liberian *Bulinus forskalii*, *B. globosus*, and Egyptian *B. truncatus*. (Exception: Fig. 96,b is of Ghanaian stock, reared at the Museum of Zoology, The University of Michigan.)

FIGURE 91. Body form: a and c, *Bulinus globosus;* b, *B. forskalii;* and d, *B. truncatus*. The photograph (a) shows a specimen in a quiescent state as seen on the vertical side of an aquarium. The posterior end of its sole is contracted forward. In active locomotion that end would be decidedly tapered, to a point, as is shown in c. All *B. globosus* seen had such sharply pointed bodies, and in younger specimens the posterior end is even more attenuate and trails far beyond the apex of the shell during active locomotion. *B. nasutus* and *B. africanus* from elsewhere in Africa, and only seen preserved, appear to have a similarly physoid foot. No *B. forskalii* or *B. truncatus* were ever seen to have a truly pointed foot, which in both species tends to be roundly wedge-shaped behind. Both species are also represented in b and d as being in active locomotion. In that state, the pseudobranch of *B. truncatus* is seen to be placed farther forward and extended further than in the other species. It carries that organ strongly curled dorsad. When *B. globosus* is in active locomotion its body (peristomial) collar, in and near the apertural angle, tends to protrude and to outwardly overlap the peristome. In the photograph the tentacles are abnormal, a condition seemingly related to infestation of the aquarium with ostracods. The white shell-varix is a fairly common feature of Liberian *B. globosus*. The drawings are freehand sketches.

FIGURE 92. Tooth morphology. *B. forskalii*. Three views of the rachidian (central) tooth are shown in a. The fluted lateral flanges of the reflection seen in the bottom drawing are perhaps always present, but are invisible from various angles. In b, 1st lateral teeth are shown, 2 from different transverse rows of the left side of the radula (1L) and one (1R) from the right side. Those from the left side are identical to the other, except for the reversed symmetry, but are oriented differently. In c, the 3rd, 8th and 9th (or? 8th) teeth to the right of the rachidian are shown. Note the blunt "button" on the end of the long base of the 8th tooth. The teeth were stripped from the radula by treatment with acetic acid, and were studied in part, as a "tooth-strew," on a microscope slide; otherwise they could not have been studied in such detail. The drawings are freehand sketches.

FIGURE 93. Structure of rachidian, a, and 1st lateral teeth, b, of *B. globosus*. Freehand sketches made from a partial "tooth-strew." In a, as in b, several teeth from different rows are shown oriented as they were found to be, lying in the strew. The "front" view shown on the upper left in a shows prominent lines of light-diffraction around the reflection. The side view to its right is somewhat of a reconstruction, largely based on the other drawings, and may not be entirely accurate in some respects. The tooth on the lower right in a shows no fluted flanges, although they were probably present. Note that in b, the tooth on the upper left is just as prominently cusped as those in the other drawings, but does not appear so because of its different orientation.

FIGURE 94. The 9th, 11th, 12th and 14th teeth to the right of the rachidian, in *B. globosus*. Freehand sketches made from a partial tooth-strew. Teeth from 2 different transverse rows are represented by 12′ and 12″. Note the partly doubled large "button" on the end of the base of tooth 14.



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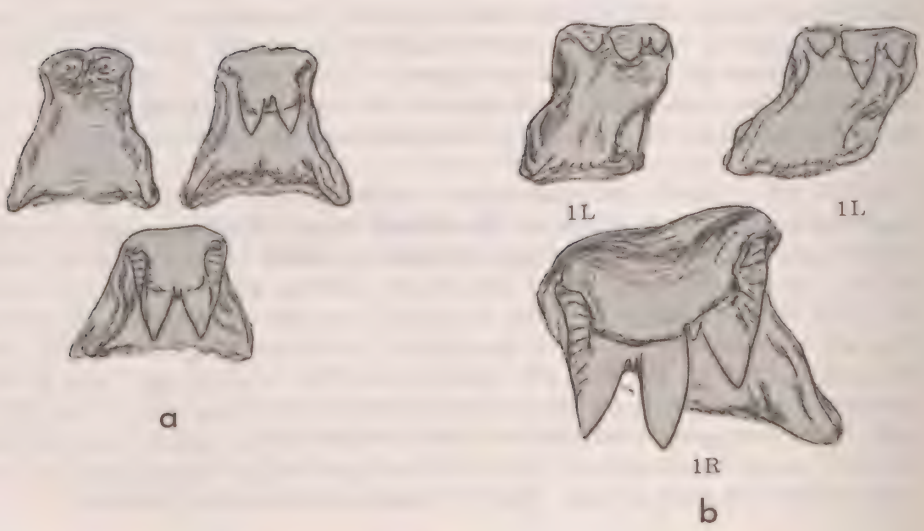
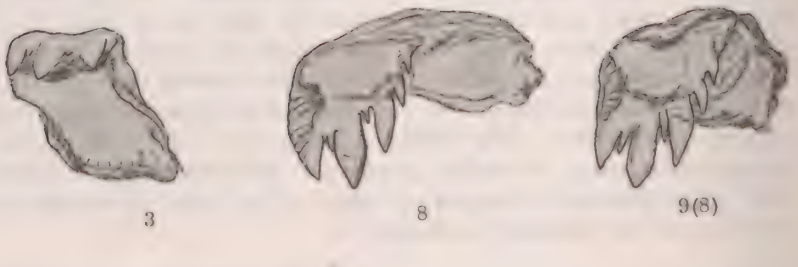




92

a

b

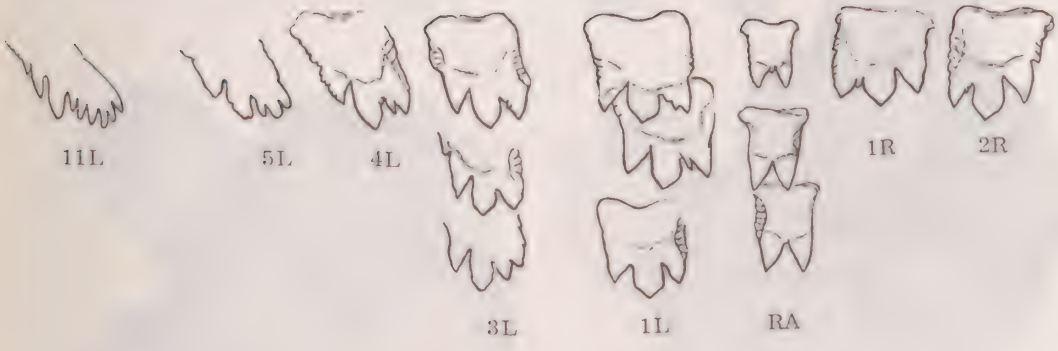
93

FIGURE 95. Teeth of *B. truncatus*, drawn as "optical tracings" with a drawing apparatus, from a radula partly stripped of its teeth. The exact shape of major cusps may have special comparative significance in systematic questions ranging beyond the limits of the Planorbidae. Some of the marginal teeth are shaped very much like tooth 14 (Fig. 94) of *B. globosus*. Ra = rachidian tooth row.

FIGURE 96. Shells of *B. forskalii*. a, 2 shells, lab-reared, are shown, the one on the left of a 1st laboratory generation, the other of a subsequent generation, perhaps several generations removed. The 1st specimen shows the "wild type" of sculpture, in which prominent axial ribs occur on all postembryonic whorls. In laboratory populations, with successive generations, the ribs and the rough and complex intercostal microsculpture tend to become obsolete, firstly on the later, larger adult whorls, and then progressively toward the spire. This condition, at its observed extreme, is exhibited by the specimen on the right. Even the shoulder carina tends to become obsolete. However, it appears that the normal "wild" sculpture always persists on the upper spire whorls, at least on the 2nd whorl. In b the embryonic microsculpture of an adult shell is shown. The punctae are deep, narrowly conical pits. A rather intricate ultrafine sculpture exists in the space between the punctae and is barely visible in the photo. The embryonic 1st whorl is about 0.5 mm wide. In c, the punctae appear as bright nodules, but only because of the effect of a variation in the angle of incidence of light passing through the shell. This photo demonstrates that punctae are continuously distributed over at least the larger part of the postembryonic 2nd whorl, which appears always to be the case. Note that the punctae tend to be arranged in 2 axial rows between each pair of ribs, and that they tend to occur in the edges of the ribs. This shell shows a prominent erosional scar on the embryonic whorl. The apex of the larger shell in a is largely eroded away. In d, the embryonic sculpture again appears somewhat different because of a lighting effect. Note the indications of complex intercostal microsculpture. Note how some of the nuclear punctae appear as bright dots. Shell e is the same as shell d, and may be considered to be that of a young adult. Specimen f shows the especially dense crowding of sculptural elements that occurs regularly between 1 1/8 and 1 3/8 whorls. Unless the lighting is arranged very exactly, the details are blurred somewhat, as shown. So blurred, the sculpture superficially resembles the finer embryonic sculpture of *Camptoceras hirasei* and *Physastra* species, which have no punctae whatsoever. The shells were all stripped of their periostracum by the application of sodium hypochlorite. All were photographed by transmitted light while they were suspended in an agar gel.

FIGURE 97. Embryonic and juv. shells of *B. forskalii*. a, as in b, were photographed *en mass* as a shell-strew, and are cut-outs from a single photograph. Shells of the size of those in a are exceedingly fragile, and so thin that the punctae actually cannot be deep. Somehow, as these whorls thicken greatly with growth of the shell, the punctae become deep. The snails hatch when the shell has grown to about 1 1/8 whorls. Those represented in the bottom row, a, probably had hatched some days before being photographed. The smallest shell has nearly 1 whorl. The largest has about 1 1/2 whorls, and is about 1 mm long. It has just as prominent a sculpture as the one next to it, but it was on the darker periphery of the visual field of the microscope, and a consequent lighting effect caused the punctae to be invisible. Note the dense punctation in the shell next to it, a condition characteristic of the early part of the 2nd whorl. The shells in b have grown to a larger size, but were photographed at a

94



95

a

b

c

d

e

f

96

a

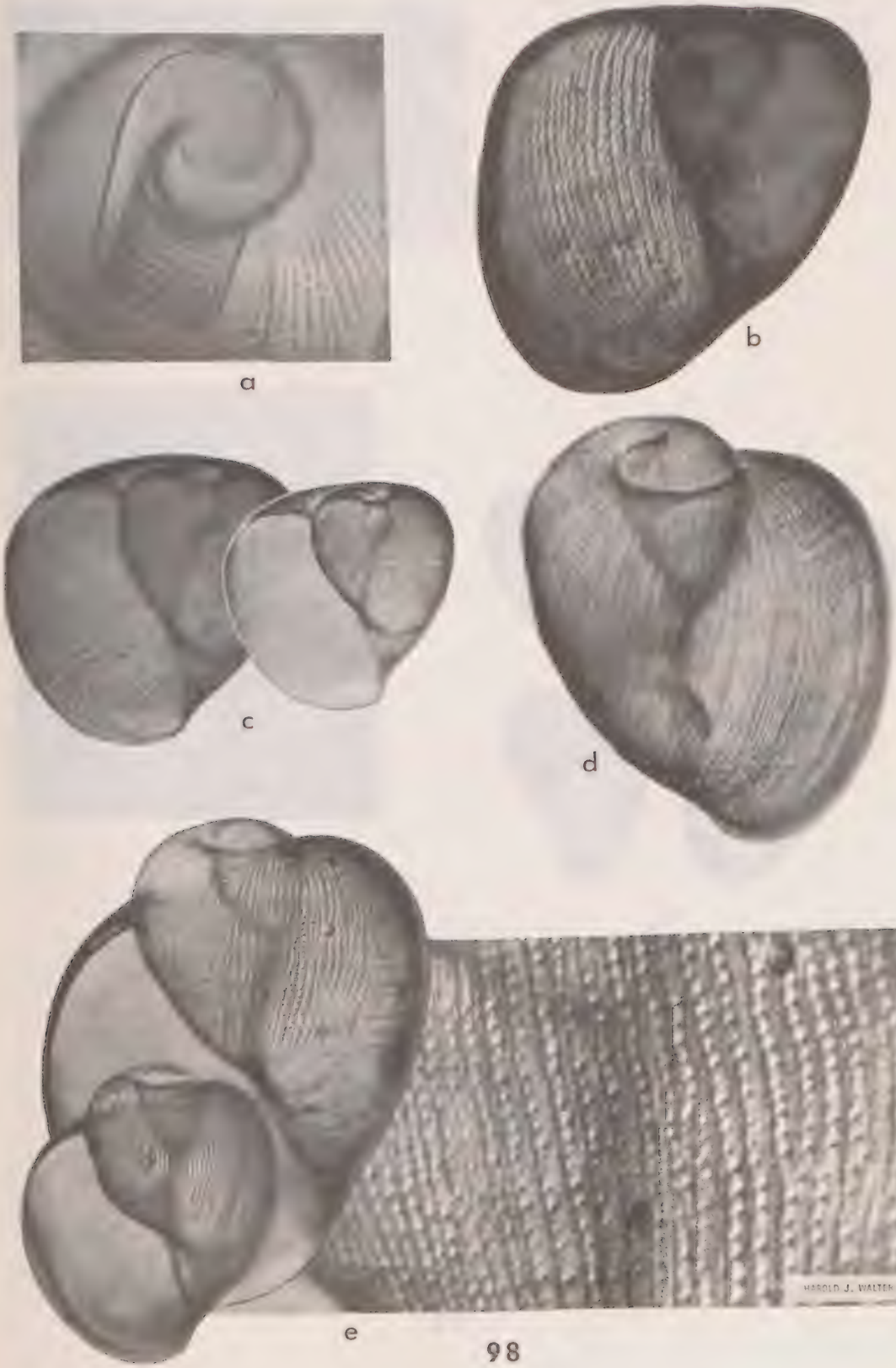
b

97

lower magnification. Their whorl count ranges from about 1 3/4 to 2 1/4. Note that one shows a distinct shoulder angle. Specimens represented in both a and b were hatched from eggs laid in the laboratory. The shells have been stripped of their periostracum and are seen by transmitted light.

FIGURE 98. *B. globosus*. A composite of 2 photos of the embryonic whorl in 2 different planes of focus, is given in a. The picture has been slightly retouched. The first part of the embryonic whorl is practically smooth, but faint punctae arise at about 1/4 whorl. Axial microriblets arise before the end of the first whorl, and the sculpture abruptly coarsens at 1 1/8 whorls. What may appear to be nodules in the photo are deep pits set in the leading, or abapical scalloped edge of the axial riblets. The total sculptural relief appears to be the reverse of what it actually is (at least to my eyes). By rotating the photo, or by holding it in front of a mirror one may see a striking reversal of the optical illusion, and clearly recognize the true nature of the sculpture. A shell of about 1 1/4 whorls is shown in b. Here the sculpture is seen through the inner wall of the far periphery of the shell and it looks (to me, at least) like it actually is, in character. Rotating or reversing the photo will yield the reverse optical illusion. Two photos of a single shell of about 1 1/2 whorls are given in c. In the more magnified view the focus is on the far periphery of the shell, and in the other, on the near periphery. A shell of about 1 3/4 whorls is shown in d. It indicates how the basic sculptural pattern visible in a, b, and c, continues far beyond the nuclear whorl. Two shells of about 2 whorls are shown in e, at different magnifications. A much greater enlargement of the sculpture visible in the more magnified shell is given. The sculptural enlargement should be rotated to demonstrate the optical illusion presented. Neither of the 2 shells are very typical in form, the more magnified one being more regularly rounded than is usual. The other shell was from a snail reared in an aquarium very heavily infested with ostracods, and it is definitely distorted and evidently somewhat stunted. This snail's aquarium-mates generally showed a very similar distortion. The shell is abnormally squat for its size, and shows a peculiar bulging of the parietal wall. All shells in the figure are from aquarium populations; they were photographed by transmitted light after being stripped of their periostracum.

FIGURE 99. *B. truncatus*. a, an embryonic shell (ca. 1 whorl). It is sculptured as markedly as specimen b, although it does not show it because of a lighting effect. At this early stage it already shows the deep suture and the notable arching of the adapical region of the whorls, features which are characteristic of the later whorls. Photograph b, on inspection, will demonstrate that the punctae are pits; near the middle of the exposed portion of the nuclear whorl the focus is in the depth of the pits; more peripherally, the focus is on their wider outlets at the shell-surface. Juvenile shells are shown in c, as cutouts from a single picture taken of a shell-strew. Their whorl count ranges from about 1 1/4 to about 1 3/4. A decided pattern of well-spaced axial ribs becomes developed at 1 1/8 whorls, although it hardly shows in these photos. In d, the picture is a composite of 2 photographs made in 2 different focal planes. Damage to the photo has been retouched. The shell shows the well-spaced ribs becoming prominent at 1 1/8 whorls, and shows the characteristic ultrafine "etched" spiral striolation between the ribs. This striolation passes over the ribs and over a somewhat evenly regular sculpture of intercostal fine subriblets. All photos in this figure were taken by transmitted light, except for those in e, wherein 2 juvenile shells are shown. The last 2 overlapping photos are of the same shell, made under slightly different lighting con-



98

a

b

c

d

e

ditions. They show that the rib-sculpture is really rather prominent and regular. The ribs continue onto the body whorl in adults, and tend to be paired, somewhat irregularly. The shells of *B. forskalii* and *B. globosus*, despite their coarser and more elaborate sculpture are equally shiny. All shells in the figure have been stripped of their periostracum.

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HISTOGENESE DES MUCOCYTES DE LA GLANDE ET DE LA SOLE PEDIEUSES D'*ARION RUFUS* (STYLOMMATOPHORA: ARIONIDAE)

Danièle Binot et Monique Chetail

Récemment nous avons étudié les particularités histochimiques des mucocytes de la glande et de la sole pédieuses d'*Arion rufus* (Linnaeus) (Chetail & Binot, 1967). Ce travail nous a permis d'apporter les précisions suivantes:

La glande pédieuse comporte 2 régions anatomiques, antérieure et postérieure, auxquelles correspondent 2 types de mucocytes histochimiquement distincts. Les mucocytes a de la région antérieure élaborent des mucopolysaccharides acides complexes associés à des lipides complexes; leur forme jeune correspond au type a_1 et leur forme évoluée au type a_2; les mucocytes de type b situés postérieurement secrètent des mucoprotides dont la partie muqueuse est constituée par des mucopolysaccharides simples.

La sole pédieuse possède 4 types de mucocytes nettement distincts: ceux de type I contiennent des mucopolysaccharides simples peu acides, des mucopolysaccharides acides complexes et des lipides complexes; ceux de type II émettent des mucopolysaccharides simples et complexes, ceux de type III des polysaccharides acides et des lipoprotéines, enfin ceux de type IV produisent des mucoprotides dont la partie muqueuse est peu acide.

Pour déterminer la date d'apparition des caractères histochimiques propres à chacun de ces types de cellules muqueuses, et surtout pour essayer de résoudre le problème de leur origine nous avons suivi leur développement embryonnaire chez *Arion rufus*. Une centaine d'embryons ont été fixés par les liquides de Bouin, Carnoy, Gendre O°, Ciaccio, pour cette étude qui n'a débuté qu'au 15è jour après la ponte, moment qui précède l'apparition des structures envisagées ici, si le développement a lieu à 15°C. Les coupes d'embryons ont été traitées par les techniques qui nous ont donné les résultats les plus significatifs au cours de l'étude histochimique de ces mêmes formations glandulaires chez l'*Arion* adulte, à savoir: hémalun picro-indigo-carmin, vert de méthyle pyronine complété par le test de Vendrely, réaction à l'A.P.S.[1] contrôlée par le test à la digestion salivaire, bleu de toluidine selon Lison avec gamme de pH, bleu Alcyan, fuschine paraldéhyde avec et sans oxydation, mucicarmin de Mayer, enfin, réactions de Ciaccio et de Salazar.

RESULTATS

Au 15° jour il n'existe aucune différenciation au niveau de la future glande pédieuse et de son canal. Par contre l'ébauche de la sole pédieuse est en place. La face plantaire, au lieu de l'épithélium simple cilié typique du pied de l'adulte, est revêtue par un ectoderme pluristratifié où l'on observe des cellules en mitoses; les cellules au repos ont un cytoplasme pyroninophile et un noyau pourvu d'un gros nucléole. Au dessus de cet ectoderme se trouve un mésenchyme à cellules clair-semées dont certaines sont en division.

Du 15° au 23° jour: Le canal de la glande pédieuse se forme; il dérive d'une invagination ectodermique (Pl. 1, Fig. 6) située entre les ébauches ectodermiques de l'épithélium de la sole et du bulbe buccal. L'ébauche de ce canal possède déjà un côté dorsal mince et un côté ventral épais dont les cellules sont souvent en mitoses et, sous lequel, quelques cellules mésenchymateuses se groupent déjà (Pl. 2, Fig. 1). Le sillon latéral séparant les tissus du manteau de ceux de la sole se dessine (Pl. 1, Fig. 1). L'épithélium de la sole, feuillet ectodermique

[1] A. P. S. = Acide périodique-Schiff.

PLANCHE 1

FIG. 1. Apparition du sillon latéral séparant le manteau de la sole; 20° jour.

FIG. 2. Sole pédieuse; remarquer les mitoses dans le mésenchyme et dans l'épithélium plantaire; réaction de Feulgen, 23° jour.

FIG. 3. Sole pédieuse; apparition de la ciliature pédieuse latéralement, réaction de Feulgen; 28° jour.

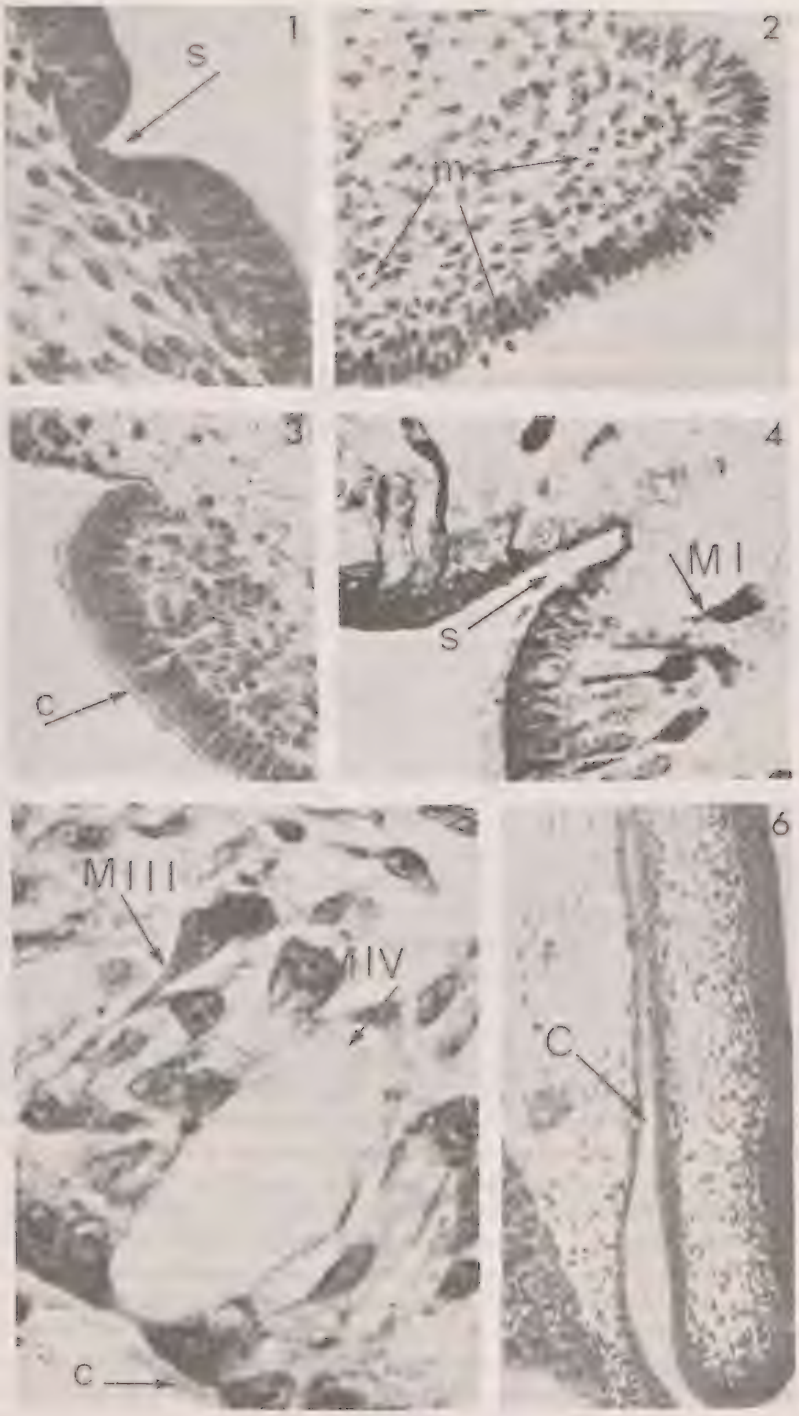
FIG. 4. Sole pédieuse; région du sillon latéral séparant le manteau de la sole; remarquer les mucocytes MI contenant des lipides complexes; réaction de Ciaccio; 33° jour.

FIG. 5. Sole pédieuse; différenciation des mucocytes MIII et MIV; Fuschine-paraldéhyde sans oxydation qui colore vivement les mucocytes MIII contrairement aux mucocytes MIV dont la sécrétion ne se colore qu'avec oxydation préalable; 35° jour.

FIG. 6. Formation du canal de la glande pédieuse par invagination ectodermique; à droite remarquer la sole pédieuse; réaction à l'A. P. S. ; 15 ème jour.

ABREVIATIONS DES FIGURES

a = mucocytes de type a; A. R. N. = acide ribonucléique; b = mucocytes de type b; C = canal; c = ciliature; ep = épithélium; j. m. = jeune mucocyte; L = lumière du canal de la glande pédieuse; m = mitose; ms = mésenchyme; M = mucocyte; MI = mucocyte de type I; MII = mucocyte de type II; MIII = mucocyte de type III; MIV = mucocyte de type IV; S = sillon latéral séparant le manteau du pied.


1
S
2
MV
3
C
4
MI
S
MIII
MIV
C
6
C

épais, devient très pyroninophile puis il s'amincit progressivement; les noyaux des cellules se dressent et s'enrichissent en chromatine tandis que les mitoses se raréfient: par contre, dans le mésenchyme sus-jacent qui s'est densifié les divisions sont fréquentes (Pl. 1, Fig. 2).

Du 23° au 25° jour: La partie dorsale du canal de la glande pédieuse se transforme en un épithélium cubique simple caractérisant le manteau, dans sa partie ventrale c'est un feuillet encore pluristratifié dans lequel les cellules riches en A.R.N. possèdent des noyaux qui commencent à se dresser (Pl. 2, Fig. 2). Au niveau de la sole, le sillon latéral délimitant cette dernière et le manteau s'accentue. L'ébauche ectodermique de l'épithélium de la sole ne présente pas de changement sensible par rapport au stade précédent; entre cette ébauche et celle de la partie ventrale du canal de la glande pédieuse, qui constituera le canal proprement dit de cette glande, se trouvent des cellules mésenchymateuses en voie de multiplication active à partir desquelles vont se différencier ultérieurement les mucocytes de la glande et de la sole pédieuses (Pl. 1, Fig. 2 et Pl. 2, Fig. 2).

Du 25° au 28° jour: Dans la région antérieure, les cellules mésenchymateuses, groupées sous le canal de la future glande pédieuse présentant toujours le même aspect, s'enrichissent en ribonucléines pyroninophiles; en fait ce sont des mucocytes a_1, c'est-à-dire de jeunes cellules a n'ayant pas encore leurs caractères histochimiques propres (Fig. 1 et Pl. 2, Fig. 3). Dans la région postérieure on n'observe toujours pas de condensation mésenchymateuse sous le canal. Tout au long du développement, ce décalage dans le temps entre la différenciation des régions antérieure et postérieure se retrouvera, très nette au niveau de la glande, moins nette, mais sensible cependant au niveau de la sole. Dans le mésenchyme de la sole on ne note pas de modifications importantes; le seul changement appréciable concerne l'A.R.N. contenu dans les cellules épithéliales de la sole qui au lieu de remplir tout le cytoplasme comme auparavant se localise au pôle apical des cellules où se différenciera bientôt la ciliature.

Du 28° au 31° jour: Dans la glande pédieuse les mucocytes de la région antérieure et moyenne acquièrent progressivement leurs caractères histochimiques propres: métachromatiques à la pyronine, ils se colorent fortement après réaction à l'A.P.S. et se chargent en lipides complexes; ce sont des mucocytes a_2 correspondant aux cellules a_1 devenues matures (Pl. 2, Fig. 4). Dans la région postérieure de la glande, sous son canal, se condensent des cellules mésenchymateuses (Pl. 2, Fig. 5) se multipliant par mitoses; c'est exactement ce que l'on pouvait observer au stade précédent dans la région antérieure de cette glande. Dans la portion latéro-antérieure de la sole, la ciliature épithéliale apparait graduellement, tandis qu'au sein du mésenchyme les cellules voient chacune leur noyau et leur nucléole s'accroître, leur cytoplasme s'enrichir en A.R.N. et se charger d'une sécrétion prenant peu à peu les caractères suivants: A.P.S. positive, elle se colore vivement après réaction de Ciaccio, prend fortement le mucicarmin et le bleu alcyan: ce premier type formé correspond aux mucocytes I (Fig. 2 et Pl. 1, Fig. 4); ces cellules muqueuses, encore rares à ce stade, se localisent à la partie antérieure de la sole surtout au niveau du sillon latéral séparant le manteau du pied, zone où elles sont particulièrement abondantes chez l'adulte. Dans la partie postérieure de la sole, épithélium plantaire et mésenchyme sont toujours indifférenciés et poursuivent leur multiplication par mitoses. A ce stade le gradient antéro-postérieur de différenciation devient donc particulièrement sensible qu'il s'agisse de la glande ou de la sole pédieuses, puisque seuls les mucocytes les plus antérieurs a pour la glande et I pour la sole sont alors observables.

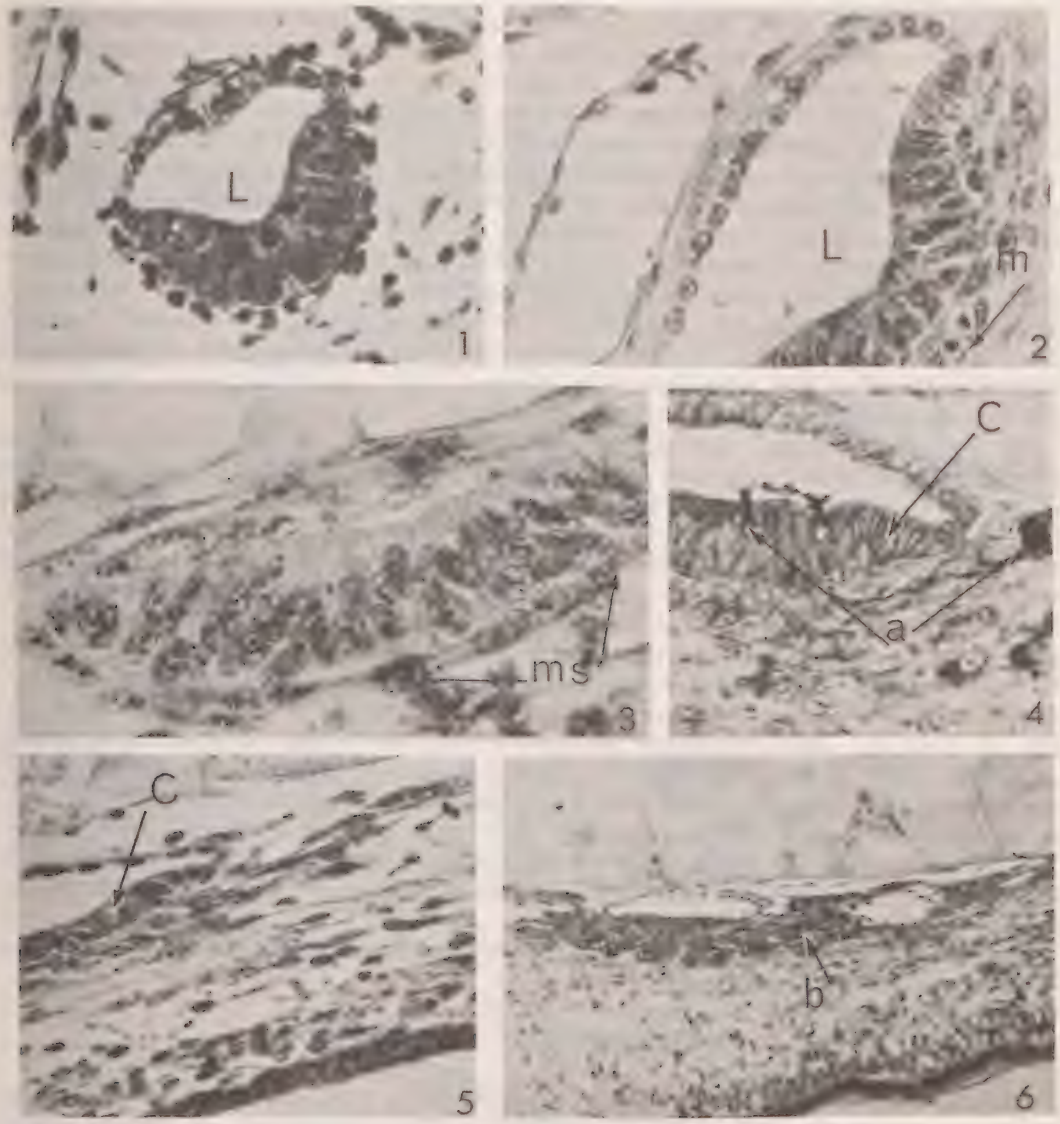


PLANCHE 2

FIG. 1. Glande pédieuse (région antérieure); coupe transversale au niveau du canal de la glande; réaction à l'A. P. S. ; 20° jour.

FIG. 2. Glande pédieuse (région antérieure); demie coupe transversale de la glande pédieuse; remarquer le mésenchyme plus dense où s'observe des mitoses; Vert de Méthyle-Pyronine; 23° jour.

FIG. 3. Glande pédieuse (région antérieure); réaction de Feulgen; 25° jour.

FIG. 4. Glande pédieuse (région antérieure); demie coupe transversale montrant des mucocytes de types a; réaction de Ciaccio pour les lipides complexes; 28° jour.

FIG. 5. Glande pédieuse (région postérieure); demie coupe transversale montrant le canal de la glande sous lequel s'accumule des cellules mésenchymateuses; Hémalun picro-indigo-carmin; 31° jour.

FIG. 6. Glande pédieuse (région postérieure); coupe transversale; remarquer sous le canal les mucocytes b qui commencent à se différencier; Hémalun picro-indigo-carmin; 33° jour.

Du 31° au 33° jour: dans la portion la plus antérieure du canal de la glande pédieuse la ciliature se forme peu à peu; elle est encore absente postérieurement. Quant à la glande proprement dite, sa partie postérieure prend de l'importance et durant son accroissement on observe les mêmes faits que durant celui de sa région antérieure: les cellules mésenchymateuses groupées sous le canal après s'être enrichies en ribonucléines adoptent graduellement les caractères histochimiques propres aux mucocytes de type b (Pl. 2, Fig. 6): d'abord acidophiles aux stades peu différenciés, ces cellules répondent ensuite positivement à la réaction à l'A.P.S. et à celle de Salazar. Au niveau de l'épithélium de la sole, la ciliature continue sa différenciation progressive de l'avant vers l'arrière. Au sein du mésenchyme dans la région antérieure et médiane de la sole apparaissent quelques mucocytes de type II (Fig. 3); assez rares au début ils deviennent de plus en plus nombreux pendant que s'achève leur différenciation histochimique: positivité à l'A.P.S. et métachromasie au bleu de toluidine.

Du 33° au 35° jour: La glande pédieuse et son canal ont maintenant terminé leur développement aussi ces formations se présentent elles sensiblement sous le même aspect que chez l'adulte. L'épithélium de la sole possède sur presque toute sa surface la ciliature qui la caractérise. C'est alors, qu'à partir de cellules mésenchymateuses de la sole les 2 derniers types de mucocytes manquant encore vont se former. D'abord apparaissent des cellules granuleuses qui prennent la fuschine paraldéhyde sans oxydation, sont A.P.S. positives et basophiles non métachromatiques après réaction de Lison; il s'agit des mucocytes de type III (Fig. 4). Ensuite se forment les mucocytes de type IV qui prennent fortement la fuschine paraldéhyde avec oxydation se colorent par le mucicarmin et sont Salazar positives (Pl. 1, Fig. 5). Simultanément les mucocytes I et II déjà apparus s'accroissent numériquement. A ce stade la sole possède donc les 4 types de mucocytes qui la caractérisent et qui tous émettent déjà leur sécrétion entre les cellules de l'épithélium plantaire. Jusqu'à l'éclosion (42^{e} jour environ si le développement a lieu à 15° C), qu'il s'agisse des mucocytes de la glande pédieuse ou de ceux de la sole, chacun des 6 types décrits s'accroît en taille et en nombre tout en parachevant sa différenciation histochimique.

Le Tableau 1 retrace les différentes étapes du développement de la glande et de la sole pédieuses d'*Arion rufus*.

DISCUSSION ET CONCLUSION

Au cours du développement embryonnaire de la région pédieuse d'*Arion* nous avons pu montrer qu'il existe un gradient antéro-postérieur de différenciation sensible tant au niveau de la glande que de la sole pédieuses puisque dans les 2 cas ce sont les mucocytes les plus antérieurs (a pour la glande et I pour la sole) qui apparaissent en premier. Ce même gradient antéro-postérieur se retrouve lors de la formation de la ciliature portée par l'épithélium de la sole et par celui du canal de la glande.

Nos observations au cours de l'histogénèse de la glande pédieuse d'*Arion* montrent que dans cette formation le canal et les mucocytes n'ont pas la même origine: le canal provient d'une invagination ectodermique impaire et médiane tandis que les mucocytes tirent leur origine du mésenchyme au sein et à partir duquel ils se différencient progressivement; la même dualité se retrouve d'ailleurs au niveau de la sole dans laquelle l'épithélium plantaire est d'origine ectodermique et dont les mucocytes proviennent de cellules mésenchymateuses. Des résultats différents des nôtres ont été obtenus par plusieurs auteurs notamment au cours d'études sur l'histogénèse de la glande pédieuse de divers autres mollusques: c'est ainsi

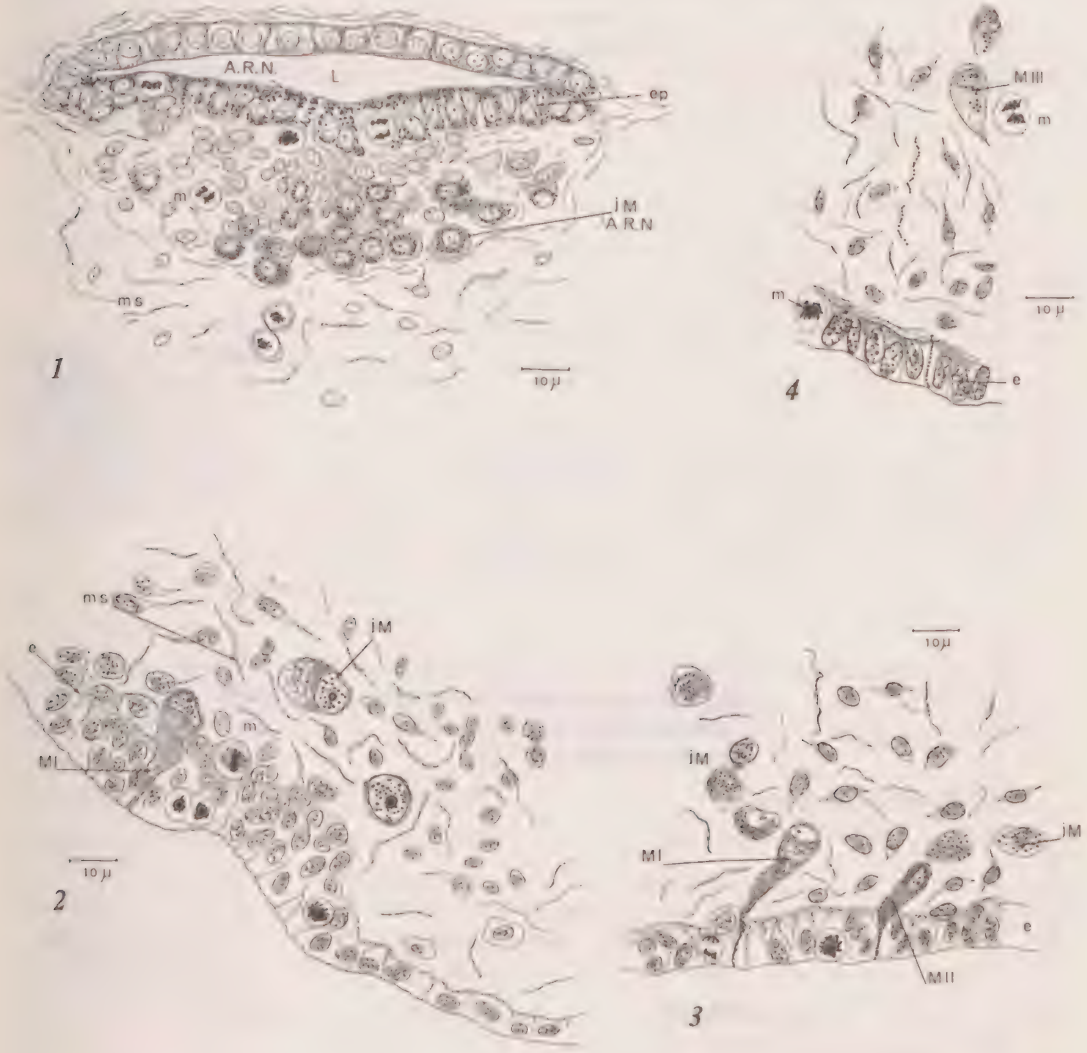


FIG. 1. Coupe transversale de la région antérieure de la glande pédieuse, remarquer la richesse des jeunes mucocytes en A. R. N. ainsi que la présence de mitoses dans le mésenchyme et l'épithélium du canal; 26° jour.

FIG. 2. Région latérale du pied montrant la formation de jeunes mucocytes I; 28° jour.

FIG. 3. Milieu de la sole pédieuse dont l'épithélium est encore dépourvu de cils; mucocytes I et II et leur évolution; 33° jour.

FIG. 4. Sole pédieuse; évolution des mucocytes de type III; 35° jour.

TABLEAU 1.

Principales étapes du développement de la glande et de la sole pédieuses d'*Arion rufus*

	Stades	15 Jours	de 15 à 23 Jours	de 23 à 25 Jours
GLANDE PEDIEUSE	Épithélium du canal	0	Ébauche du canal par invagination ectodermique Mitoses + Ciliature 0	Région apicale de l'épithélium riche en A. R. N. Mitoses + Ciliature 0
	Mucocytes	0	0	Début de condensation de cellules mésenchymateuses sous l'ébauche du canal dans la région antérieure
SOLE PEDIEUSE	Épithélium plantaire	Épithélium = feuillet ectodermique pluristratifié Mitoses ++ Ciliature 0	Apparition du sillon latéral Pyroninophilie ++ Mitoses + Ciliature 0	Accentuation du sillon latéral Pyroninophilie ++ Mitoses + Ciliature 0
	Mucocytes	Mésenchyme clair-semé Mitoses ± Mucocytes 0	Densification du mésenchyme Mitoses ++ Mucocytes 0	Densification du mésenchyme Mitoses ++ Mucocytes 0

qu'en ce qui concerne *Agriolimax* le travail de Carrick (1938) est favorable à une origine ectodermique du canal et des mucocytes de la glande pédieuse; ces derniers se forment à partir des cellules ectodermiques du canal lequel court parallèlement à la sole et en occupe une bonne moitié. De même Ghose (1963) a montré que le canal et les cellules muqueuses de la glande pédieuse d'*Achatina fulica* dérivent d'ébauches ectodermiques paires qui ne se réunissent que secondairement en une formation unique.

Tableau 1. (suite)

de 25 à 28 Jours	de 28 à 31 Jours	de 31 à 33 Jours	de 33 à 35 Jours	de 35 à 42 Jours
A. R. N. ±				
Mitoses +	Mitoses +			
Ciliature 0	Ciliature 0	Ciliature clair-semée	Ciliature dans toute la région antérieure	Ciliature gagnant la région postérieure
Cellules mésenchymateuses A. R. N. +	Mucocytes a_1 et a_2	Mucocytes a_1 et a_2		
= Jeunes Mucocytes a_1	Mitoses dans les régions latérales de la glande pédieuse (=zones des cellules a_1)	Condensation de cellules mésenchymateuses	Différenciation des cellules b dans la région postérieure	Différenciation complète des cellules a et b
	Mitoses dans la région postérieure	A. R. N. + dans la région postérieure		
Pyroninophilie apicale de l'épithélium	Apparition de la ciliature sur les côtés	Ciliature s'étendant vers le milieu de la sole	Ciliature s'étendant vers le milieu de la sole	Différenciation complète de la ciliature
Mitoses +	Mitoses +			
Ciliature 0				
Densification du mésenchyme				
Mitoses +	Mitoses +	Mitoses +	Augmentation du nombre des mucocytes I et II	Apparition mucocytes IV
Mucocytes 0	Jeunes mucocytes I riches en A. R. N.	Mucocytes I et jeunes mucocytes II riches en A. R. N.	Apparition des mucocytes III	Différenciation complète des 4 types

Par contre les recherches de Delsman (1914) sur *Littorina*, Smith (1935) sur *Patella* et Crofts (1938) sur *Haliotis* sont en faveur d'une origine mésenchymateuse de la glande pédieuse chez ces 3 espèces. Il semble que chez *Arion* se trouve réalisée une situation moyenne.

S'il est très facile d'affirmer l'origine ectodermique de l'épithélium du canal de la glande pédieuse et de celui de la sole la preuve de l'origine mésenchymateuse des mucocytes est plus difficile à apporter et c'est sans doute pourquoi ce

problème malgré les nombreuses controverses qu'il a suscitées, n'a pas encore vraiment obtenu de réponse jusqu'ici: Pour Bernard (1890) les mucocytes ne sont que des cellules épithéliales nettement différenciées. Prenant (1922, 1924) insiste sur l'origine conjonctive de ces éléments; Roth (1929) est comme Bernard partisan de l'origine épithéliale de l'élément muqueux. Les observations de Froutin (1937) portant sur un grand nombre de Gastéropodes sont plutôt favorables à la thèse de Prenant. Binot (1965) étudiant la régénération des mucocytes de la sole d'*Onchidella celtica* était arrivée à la même conclusion. Ce travail apporte donc une confirmation à la thèse de Prenant en contradiction avec celle de Roth et Bernard. Cependant, d'après certaines de nos observations non publiées, il n'est pas impossible de concilier les 2 points de vue, en s'adressant à des Prosobranches tels *Ocinebra erinacea*, *Thais lapillus* ou *Nassarius reticulatus* dont le pied possède, outre des mucocytes sub-épithéliaux vraisemblablement d'origine mésenchymateuse, des cellules caliciformes situées dans l'épithélium plantaire même pour lesquelles il parait logique d'admettre une origine épidermique. Une étude de la régénération et du développement embryonnaire de ces 2 types de cellules muqueuses, chez l'un de ces trois Prosobranches permettrait sans doute de confirmer ou d'infirmer ce point de vue.

RESUME

L'étude histochimique de l'histogènèse de la glande et de la sole pédieuses d'*Arion* aboutit aux résultats suivants:

La glande pédieuse a une double origine: son canal provient d'une invagination ectodermique impaire et médiane tandis que ses cellules glandulaires à mucus se forment à partir du mésenchyme. Les mucocytes (a) les plus antérieurs apparaissent en premier tandis que les mucocytes (b) situés postérieurement se différencient plus tard.

Cette dualité se retrouve au niveau de la sole pédieuse dont l'épithélium plantaire dérive de l'ectoderme et dont les 4 types de mucocytes proviennent de la différenciation progressive de cellules mésenchymateuses. Durant toute l'histoténèse des formations étudiées il existe un gradient antéro-postérieur de différenciation. Nos résultats sont comparés avec ceux de Carrick (1938) sur *Agriolimax agrestis*, Ghose (1963) sur *Achatina fulica*, Delsman (1914) sur *Littorina obtusa*, Smith (1935) sur *Patella vulgata* et Crofts (1938) sur *Haliotis tuberculata*. Chez *Agriolimax* et *Achatina* la glande pédieuse est ectodermique tandis que chez *Littorina*, *Patella* et *Haliotis* elle est mésodermique. La glande et la sole pédieuses d'*Arion* offrent l'exemple d'un compromis entre les deux thèses: origine ectodermique pour l'épithélium plantaire et celui de canal glandulaire et origine mésenchymateuse pour les cellules à mucus.

ABSTRACT

The histochemical study of development of the pedal gland and sole in *Arion* gives the following results.

The pedal gland has a double origin: its duct comes from a single and median ectodermal invagination, while the 2 kinds of mucocytes of the gland itself arise from the differentiation of mesenchymatous cells; mucocytes a, at the anterior part of the gland are the first to appear, while mucocytes b, located at the posterior part of the gland, appear later.

At the level of the sole one can find again the same dual origin: ectodermal for the sole epithelium and mesodermal for the 4 kinds of mucocytes, the most anterior

of which are differentiated first. During the whole development this antero-posterior gradient of differentiation can be recognized for the pedal gland as well as for the sole itself.

Our results are compared with those of Carrick (1938) in *Agriolimax agrestis*, Ghose (1963) in *Achatina fulica*, Delsman (1914) in *Littorina obtusa*, Smith (1935) in *Patella vulgata* and Crofts (1938) in *Haliotis tuberculata*. In *Agriolimax* and *Achatina*, the pedal gland is ectodermal in origin, while in *Littorina*, *Patella* and *Haliotis*, this formation is mesodermal. In *Arion* the pedal gland and sole show a compromise between the 2: there is an ectodermal origin for the epithelium of the sole and duct of the pedal gland, and a mesenchymatous origin for the mucocytes in these 2 tissues.

ZUSAMMENFASSUNG

Die histochemische Untersuchung der Enstehung an der Sohle sovie an der Fussdrüse des Arion gibt zu folgenden Schlussfolgerungen Anlass:

Die Fussdrüse hat einen doppelten Ursprung: ihre Röhre bildet sich durch Einstülpung, welche von einem äusseren Keimblatt ausgeht, während ihre drüsenartigen Schleimzellen von mesenchymatischen Zellen ausgehen. Die worderen Schleimzellen a erscheinen als erstere während die Schleimzellen b, die sich an der hinteren Seite befinden, sich erst später absondern.

Diese Dualität erscheint ebenfalls in der Fussohle, deren Epithelium von dem äusseren Keimblatt herrührt während deren 4 Typen von Schleimzellen sich durch die fortschreitende Absonderung der mesenchymatischen Zellen bilden. Während des ganzen histochemischen Bildungsprozesses ist eine steigerung in der Zellenbildung festzustellen, welche sich von der Vorderseite nach der Hinterseite hin vollzicht.

Unsere Schlussfolgerungen worden vergliechen mit der Befunden von Carrick (1938) über den *Agriolimax agrestis*, von Ghose (1963) über *Achatina fulica*, von Delsman (1914) über *Littorina obtusa*, von Smith (1935) über *Patella vulgata* und von Crofts (1938) über *Haliotis tuberculata*. Bei *Agriolimax* und *Achatina* bildet sich die Fussdrüse von einem äusseren Keimblatt aus, bei *Littorina*, *Patella* und *Haliotis* hingenen ist sie mesodermischer Natur. So mit sind die Fussdrüse wie auch die Fussohle des *Arion* ein Beispiel eines Kompromisses zwischen beiden Thesen: einerseits ectodermischer Ursprung des Epithels des Fussohle und der Drüsenkanals; andererseits, mesenchymatischer Ursprung der Schleimzellen.

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SUR LES VARIATIONS DE *LITTORINA SAXATILIS*. EXEMPLE DE DISTRIBUTION D'UNE VARIÉTÉ DONNÉE[1]

E. Fischer-Piette et J.-M. Gaillard

La variabilité intra-spécifique, bien qu'ayant jusqu'ici moins accaparé l'attention et les efforts des zoologistes que la spécificité, par laquelle il fallait bien commencer, n'est pas moins intéressante et importante, pour elle-même, pour l'écologie, pour l'étude de l'évolution des peuplements et de l'évolution tout court.

Une des espèces les plus variables qui soient est *Littorina saxatilis* Olivi. L'étude de sa variation, commencée par Dautzenberg & Fischer (1912, p 187) a été continuée par nous (voir index bibliographique) et s'est montrée si complexe et si copieuse, qu'il nous a bien fallu procéder de manière fractionnée, selon les possibilités qui s'offraient à nous et sans même avoir pu bâtir au départ un ordre logique dans la foule des problèmes qui se levaient devant nous.

Dans nos recherches, qui sont surtout à tendance écologique, nous avons en somme, jusqu'ici, analysé des populations de points abrités, principalement dans des estuaires et rias (Rance, Odet, Ria del Barquero, de Camariñas, de Vigo), les points battus de la côte ibérique, et fait la monographie d'une petite île bretonne, l'île Hoedic.

Dans le présent article, au lieu de prendre un facteur donné ou une localité donnée, nous voulons prendre une variété donnée et faire connaître sa distribution le long des côtes de l'ancien continent depuis la frontière soviétique jusqu'au détroit de Gibraltar, et cela à titre de premier exemple, de base de comparaison.

Nous sommes en mesure de le faire. Sur ces 9.000 km de côtes nous avons récolté nous-mêmes, et examiné, 105.670 exemplaires de *Littorina saxatilis* provenant de 619 stations ce qui fait une moyenne de 171 exemplaires par localité.

La variété choisie est celle qui est constituée par des individus de couleur rouge et cela pour une raison simple et de caractère personnel. Ce sont les populations rouges qui sont à l'origine de nos études sur *Littorina saxatilis*, du fait que, dès que l'aîné de nous deux commença sa carrière de biologiste marin en étant nommé en 1926 au Laboratoire maritime du Muséum situé près de Saint-Malo, il se demanda pourquoi certains îlots ou pitons de la région présentaient des populations rouges (pratiquement homogènes), si la cause devait en être cherchée dans des faits d'isolement, et conçut dès lors le projet de porter sur le plan écologique l'étude de la variation de *Littorina saxatilis* commencée par Dautzenberg & Fischer en 1912.

Dans le présent travail nous considérons tous les individus rouges comme appartenant à une seule variété, la variété *rubescens* Monterosato (1878, p 83). Nous laisserons donc de côté les dénominations *sanguinea* Dautzenberg & Durouchoux (1900, p 8) et *miniata* Dautzenberg & Fischer (1912, p 199).

Il nous faut situer la frontière entre les variétés *aurantia* et *rubescens*. Employant le code de Seguy (1936), nous considérerons comme appartenant à la var. *rubescens* les individus ayant la teinte du n° 182 (qualifié "terre cuite" par Seguy) et tous ceux qui sont d'une teinte plus rouge.

ENONCE DES RESULTATS

Avant d'énumérer les données recueillies, du Nord au Sud, faisons savoir que nous procédons comme si tous les individus rougeâtres appartenaient à une

[1]Cette publication est la neuvième d'une série de notes intitulée "Sur les variations de *Littorina saxatilis*."

même espece. C'est d'ailleurs l'opinion la plus récente (voir Fischer-Piette, Gaillard & Delmas, 1967, p 895; James, 1968, p 143).

Nous allons donc donner maintenant la liste des stations (voir plus loin, tableau 1) où nous avons rencontré des *rubescens*, en faisant connaître pour chacune, d'une part l'essentiel des caractéristiques du milieu ambiant, et d'autre part le pourcentage des individus *rubescens* relativement à l'ensemble de la population.

Beaucoup de stations visitées ne présentent pas de *rubescens* dans les récoltes que nous y avons faites. Il serait instructif de faire connaître, pour elles aussi, les conditions ambiantes, mais cela nous entraînerait beaucoup trop loin. Afin que le lecteur puisse en tous cas connaître le nombre de stations passées ainsi sous silence, nous faisons figurer les numéros extraits de notre liste générale de travail, par ordre géographique, des stations où nous avons récolté des *Littorina saxatilis*.

COMMENTAIRES

Non-uniformité de la distribution

Le tableau des stations que nous venons de donner montre d'abord à quel point est vrai le fait, énoncé déjà ci-dessus, que les littorines rouges ne sont présentes qu'en certaines des localités où des récoltes ont été faites. Il permet en effet de compter ces stations, qui sont au nombre de 66 sur 619. Mais il y a des réserves à faire sur ce nombre. Etant donné que souvent le pourcentage des individus rouges est très faible, 1% ou encore moins, il est probable que nous aurions un plus grand nombre de stations si nous avions récolté dans chacune un plus grand nombre d'individus que nous n'avons fait. Car 105.670 individus pour 619 stations, représentent un chiffre moyen de 171 individus par station, ce qui n'est pas un grand nombre (à récolter un grand nombre d'individus en chaque station nous aurions trop appauvri beaucoup d'elles).

Mais nous n'aurions quand même pas eu d'individus rouges en toutes les stations, car il y a des régions étendues où aucun n'a pu être trouvé.

Régions de présence et d'absence (Fig. 1)

Le fait le plus frappant, à ce point de vue, est l'absence d'individus rouges sur toute la côte Ouest de la péninsule ibérique, depuis l'angle de la Galice (Camariñas) jusqu'au détroit de Gibraltar inclus.

Le détroit de Gibraltar marquant la limite Sud de l'espèce, il est permis de supposer que cette absence est due à l'impossibilité pour cette variété de vivre dans des conditions trop méridionales. Car on sait que les variétés de *Littorina saxatilis* n'ont pas toutes les mêmes possibilités physiologiques, comme cela a été montré pour les durées d'émersion ou pour la pénétration jusqu'au fond des estuaires saumâtres.

Pour ce qui est du Nord, nous avons trouvé des individus rouges jusqu'au bout du territoire exploré sur l'océan glacial. Il conviendrait donc de chercher à savoir si on les voit s'arrêter en continuant vers l'Est sur la côte russe où l'influence adoucissante du Gulf Stream s'atténue. Nous espérons pouvoir recueillir bientôt des données à ce sujet. Il faudrait aussi réunir des données concernant les populations septentrionales américaines de cette espèce.

A l'intérieur de l'aire générale de présence dont nous venons de parler, il y a des lacunes. L'une d'elles, très étendue, va de Frederikshavn (Danemark) à Flamanville (côte Ouest du Cotentin). A quoi peut-elle être dûe? La réponse est simple pour sa partie orientale: les rivages des côtes allemandes, hollandaises

TABLEAU 1.

N° de la station	Pourcentage de *rubescens*	Désignation de la station	Caractères succints du milieu ambiant
4	0,5	Route Vardö-Persfjord	Sur la mer ouverte. Modérément battue
11	3,0	Stallogargo, au revers de l'île d'Hammerfest	Bien abritée
12	1,4	Altafjord, dans le fond de la plus septentrionale des 2 branches du fjord	Très protégée, dessalure faible?
15	2,0	Bjerwik, au fond du fjord de Narwik	Très protégée, dessalure faible?
26	1,2	Frederikshavn, à 1 km au Nord du port	Sur la mer ouverte, mais peu battue
51	0,5	Flamanville, sous le sémaphore	Très battue
56	0,7	Carolles, rochers au Sud de la plage	Assez exposée (mer ouverte)
98	1,3	Dinard, sous le laboratoire du Muséum, récolte du 10 août 1965	Vagues assez faibles (entrée de la Rance)
112	1,3 0,8	Dinard, entre Port-Riou et la plage de St. Enogat: 1,3% en 1959 et 0,8% en 1965	Modérément exposée (mer ouverte)
117	96,0 90,0 93,0	St. Enogat, Grand Vidé: 96,0% en 1960, 90,0% en 1961, et 93,0% en 1965 (moyenne: 95%)	Semi-exposée (mer ouverte)
119	85,0	Ile Harbour, extrémité Nord	Très battue
120	60,0	Ile Harbour, flanc Est	Assez exposée
121	64,0	Ile Harbour, flanc Est dans un couloir étroit	Conditions particulières aux couloirs
122	48,0	Ile Harbour, flanc Sud (face à la côte)	Modérément exposée
123	50,0	Ile Harbour, flanc Ouest	Battue
124	0,9	St. Lunaire, à l'extrémité Est de la plage	Assez abritée (mer ouverte)

Tableau 1. (suite)

N° de la station	Pourcentage de *rubescens*	Désignation de la station	Caractères succints du milieu ambiant
126	2,4	Presqu'île du Décollé, sous le calvaire	Battue
135	1,3	Le Val André, Pointe de Pléneuf, versant Est	Semi-exposée
137	0,53	Pointe du Roselier (St. Brieuc), flanc Nord de l'extrémité	Exposée
138	1,9 0,7	Pointe de Pordic: 1,9% en 1959 et 0,7% en 1965	Battue
144	0,0 0,7	Pointe de Plouézec: 0,0% en 1959 et 0,7% en 1965	Exposée
145	1,0	Ile Bréhat, Phare du Paon, flanc Ouest près de l'extrémité	Battue
146	0,5	Pointe de l'Arcouest, à l'Ouest de l'embarcadère pour Bréhat	Modérément exposée
148	4,2 18,0	Sillon de Talbert, la grosse masse rocheuse située à quelques centaines de mètres du départ de la levée de galets constituant le "sillon" et à quelques centaines de mètres de cette levée: 4,2% en 1959 et 18,0% en 1965	Assez exposée
149	1,25	Kermagen, près de Pleubian, sur la rive droite de la "Rivière" de Tréguier près de son débouché	Peu exposée
161	0,57	Locquirec, Pointe à l'Ouest de la plage	Battue
169	0,50	Carantec, Pointe de Penn Ann Lann	Semi-abritée (rivière de Morlaix près de son embouchure)
176	3,6	Roscoff, Per'haridy (Sanatorium)	Semi-exposée

Tableau 1. (suite)

N° de la station	Pourcentage de *rubescens*	Désignation de la station	Caractères succints du milieu
179	0,4	Nord de Plouescat, entre St. Eden et Penfrat, sous une butte à menhir	Assez battue, mer ouverte
181	22,0	Nord de Plouguerneau, à Troulouc'h St. Michel	Battue
184	2,0	Kervigorn, exactement à l'angle de sortie de l'Aber Benoît rive gauche	Semi-exposée
186	2,6	Kersaint, au premier point où la route de Kersaint à Trémazan atteint la mer	Semi-abritée (gros blocs sur sable)
259	2,2	Quiberon, extrémité Ouest de la "Côte sauvage," devant le vivier, dans un profond couloir parallèle au front de mer	Très battue
260	7,4	Quiberon, tout près, mais au Sud-Est, (flanc du début de la "côte sauvage")	Un peu abritée (pente douce)
266	0,3	Belle-Ile, Ster Vrass, dans un diverticule du "port" (découpure barrée)	Assez exposée
278	2,3	Ile Hoedic, Beg Lagatte	Modérément exposée
281	0,2	Ile Hoedic "Port Neuf"	Modérément exposée
297	0,3	Petite crique à 180 m à l'Ouest de la Pointe de Penlan	Peu exposée
298	2,5	Pointe de Penlan	Peu exposée aux vagues; mais soumise aux courants de l'embouchure de la Vilaine
300	3,5 1,7 2,0	Piriac, saillie du centre de l'anse du sémaphore: 3,5% en 1964; 1,7% en 1965; 2,0% en 1966, moyenne: 2,4%	Assez exposée

Tableau 1. (suite)

N° de la station	Pourcentage de *rubescens*	Désignation de la station	Caractères succints du milieu ambiant
301	0,9	Piriac, paroi Sud-Est de cette anse (flanc de la pointe du Castelli)	Assez exposée
303	2,0 5,5 2,1	Pointe du Croisic, à la racine de l'épi submersible prolongeant la pointe; 2,0% en 1964; 5,5% en 1965; 2,1% en 1966, moyenne: 3,2%	Exposée
304	2,0	Le Pouliguen, Grande Côte, grève avancée à 1 km à l'Ouest de la Pointe de Penchâteau	Battue
306	0,0 1,8	Pointe de Chemoulin, sur le front de la Pointe elle-même: 0,0% en 1958; 1,8% en 1965, moyenne: 0,9%	Exposée
308	0,2	Plage de St. Marc, revers du groupe rocheux médian	Semi-abritée
309	0,0 0,5 0,9	Pointe St. Gildas: 0,0% en 1956; 0,5% en 1965; 0,9% en 1966, moyenne: 0,5%	Couloirs dans un site exposé
311	2,0 0,0	Préfailles, rochers de l'Ouest de la plage: 2,0% en 1964; 0,0% en 1965, moyenne: 1,0%	Modérément exposée
312	0,4	Préfailles, rochers de l'Est de la plage	Modérément exposés
314	14,0 2,6 2,1	Pornic, paroi Nord de la plage de la rive gauche du chenal du port: 14,0% en 1957; 2,6% en 1959; 2,1% en 1965, moyenne: 6,2%	Assez abritée, parfois légère dessalure
316	0,0 0,0 0,6	Pornic, pointe de Gourmalon: 0,0% en 1956; 0,0% en 1958; 0,6% en 1965, moyenne: 0,2 %	Semi-exposée
320	0,7	Ile d'Yeu, Pointe de la Pulante, flanc Est	Assez abritée

Tableau 1. (suite)

N° de la station	Pourcentage de *rubescens*	Désignation de la station	Caractères succints du milieu ambiant
322	0,0 0,0 4,8	Ile d'Yeu, Pointe du But, falaise devancée par une barre élevée: 0,0% en 1956; 0,0% en 1957; 4,8% en 1963, moyenne: 1,6%	Assez battue
343	5,0 2,1 0,6	Ile de Ré, sur la côte ouverte, Loix, juste à l'Est de la sortie du Fier d'Ars: 5,0% en 1955; 2,1% en 1959; 0,6% en 1965, moyenne: 2,6%	Semi-abritée parmi les pierrailles
351	0,0 0,0 0,0 10,0	Fouras, La Fumée, au S.-E. de l'embarcadère pour l'île d'Aix: 0,0% en 1955; 0,0% en 1956; 0,0% en 1958; 10,0% en 1965	Semi-abritée parmi les pierrailles
380	6,5 37,0 6,7 5,7 4,8	Castro-Urdiales, 2° anse à l'Ouest de la ville, champ de cailloux: 6,5% en 1955; 37,0% en avril 1956; 6,7% en octobre 1956; 5,7% en 1960; 4,8% en 1964, moyenne: 12,0%	Assez abritée par une barrière rocheuse
414	1,5	La Franca, côte ouverte à l'Est du petit estuaire	Exposée
415	4,5	La Franca, moins à l'Est	Exposée
416	1,2	La Franca, aux approches de l'estuaire	Semi-exposée
439	24,0	Perlora (entre Gijon et Aviles), grève sous le sanatorium, couloir de descente à l'Est	Assez exposée
440	20,0	Perlora, au sortir de ce couloir	Site exposé
441	19,0	Perlora, moins à l'Est	Site exposé
442	2,1	Perlora, moins à l'Est. Crêtes avancées	Assez exposée

Tableau 1. (suite)

N° de la station	Pourcentage de *rubescens*	Désignation de la station	Caractères succints du milieu ambiant
491	1,6	Ria del Barquero, rive Est, au côté Ouest de la Playa Xilloy	Exposée, dessalure faible
523	4,0	Ria de Camariñas, rive Nord de l'estuaire du rio del Puerto à l'angle où cet estuaire débouche dans la ria proprement dite	Vagues modérées, faible dessalure
532	2,2	Ria de Camariñas, près du fond du diverticule de l'Ensenada de la Vasa, rive droite	Abritée, dessalure faible
533	4,0	Ria de Camariñas, près du fond du diverticule de l'Ensenada de la Vasa, rive gauche	Abritée, dessalure faible

et belges de la Mer du Nord sont presque partout meubles et impropres par conséquent à l'existence d'une espèce qui rampe sur un substrat cohérent. La question ne se pose donc que du Cap Gris-Nez à Flamanville, c'est-à-dire pour la Manche orientale et pour la côte Nord du Cotentin.

On pourrait se demander si la lithologie intervient. Les roches sont très tendres dans la Manche orientale jusqu'à la baie de Seine, jusqu'au départ du Cotentin; dans cette région, les populations de *Littorina saxatilis* sont généralement très peu nombreuses (ce qui pourrait contribuer à n'avoir pas mis entre nos mains d'exemplaires rouges), et il ne serait d'ailleurs pas interdit de se demander si ces conditions particulières ne seraient pas susceptibles de contrarier certaines variétés. Mais les côtes Est et Nord du Cotentin sont de roche dure, et, si on y voit *Littorina saxatilis* redevenir abondante, les individus rouges ne reparaissent pas pour autant. En continuant vers l'Ouest nous allons trouver matière à poursuivre la discussion.

Une seconde région lacunaire va de Kersaint (angle de la Manche et de l'Atlantique) à Quiberon. Il s'agit là, comme pour les côtes Est et Nord du Cotentin, de rivages durs. Il est très déroutant de voir que dans le massif ancien du Cotentin et de Bretagne on ait d'abord une région d'absence (côtes Est et Nord du Cotentin), puis une région de présence (côte Ouest du Cotentin et côte Nord de Bretagne), puis de nouveau une région d'absence, sans qu'il y ait apparemment de différences notables, non seulement au point de vue lithologique, mais aussi pour le climat, l'hydrographie, la turbulence etc.

Mais il y a lieu de faire une remarque au sujet de l'étendue de la lacune de la côte Sud de Bretagne dont nous parlons.

En effet, dans quelques stations de la partie Nord de cette lacune, s'il n'y a pas de *rubescens* il y a des individus d'une variété qui en est très proche, la

var. *rubrolineata* Fischer, Gaillard & Delmas, décrite dans le travail de 1966 à la p 874. Elle a été décrite comme ayant des lignes spirales rouges sur fond orange, mais ici le fond est rouge, plus clair toutefois que les lignes spirales. Le contraste des 2 teintes étant faible, certains observateurs auraient pu classer ces individus dans la variété *rubescens*. La définition des variétés et de leurs séparations est pour une part, on le sait, une convention humaine. Si on n'avait pas voulu faire de séparation, les localités de Melon, le Minou, Pointe Talagrip (fond de la baie de Douarnenez) et Baie des Trépassés seraient à retrancher de la lacune. Car il s'y trouve des *rubrolineata*, dont les pourcentages respectifs vont de 0, 6% à 5,2%.

Il ne faudrait en tous cas pas considérer qu'il s'agisse simplement d'une altération régionale de caractères, car sur la côte Nord de Bretagne, où la variété *rubescens* est fréquente en beaucoup de localités, on trouve aussi des *rubrolineata* en quelques-unes: Pointe de Pontusval, Ploumanac'h, Ile Bréhat. Quoiqu'il en soit il y a une lacune qui va de la Baie des Trépassés au moins, à Quiberon.

Une autre lacune s'observe de Fouras (Charente Maritime) à Castro-Urdiales (Espagne, Vieille Castille). Mais elle est sans signification, car cette région se prête fort mal à l'existence de *Littorina saxatilis*, du fait des sables des Landes et des roches trop friables et probablement trop chauffées par le soleil du fond du golfe de Gascogne.

Régions d'abondance et de rareté (Fig. 2)

Ne considérons plus maintenant que les régions (nous ne disons pas les localités, mais les régions) d'où les Littorines rouges ne sont pas absentes. Le degré d'abondance, généralement faible, peut être fort ou très fort dans certains secteurs. Cela résulte de la lecture de notre tableau, mais ressortira mieux sur la carte de la Fig. 2.

On y voit que, presque partout, les pourcentages ne dépassent pas 8%. En fait, ils ne les dépassent que dans quelques localités, ou secteurs très étroits. Pour schématiser, nous n'avons distingué que 3 sortes de signes pour les localités où le pourcentage dépasse 8%: rayures jusqu'à 24%; lignes croisées jusqu'à 40%; noir jusqu'à 96% qui est le maximum constaté.

Les secteurs favorisés ou très favorisés sont les suivants dans l'ordre géographique:

Région de Dinard - Sillon de Talbert - Nord de Plouguerneau - Pornic - Fouras - Castro-Urdiales - Perlora.

On voit que ces localités favorisées sont franchement disséminées.

La plupart sont sur des côtes résistantes, mais les secteurs où le pourcentage est bas sont, en majorité, tout aussi résistants, et d'autre part la côte de Fouras n'est pas résistante. Les facteurs ambiants auxquels on pourrait songer ne nous aident pas non plus, ce que le caractère disséminé des stations favorisées rendait d'ailleurs presque évident a priori.

Il serait tout de même difficile de penser que le "hasard de la variabilité" au sein des populations (il ne s'agit que d'une expression commode qui ne nous avance pas) puisse être invoqué pour rendre compte de ces faits. En particulier, il doit bien y avoir une raison à l'existence des populations presque pures des environs de Dinard.

A leur sujet, faisons remarquer qu'elles se trouvent en position isolée: île Harbour, et piton du Grand Vidé qui surgit du bas de la plage de St. Enogat. Mais les populations de l'île Harbour ne sont presque pures qu'à l'extrémité battue de cet îlot, le pourcentage s'abaisse beaucoup en arrière et surtout sur la face

FIG. 1. Carte des régions de présence et d'absence de la variété *rubescens*. (Là où se trouve le mot "impossible" il s'agit de côtes ne permettant pas l'existence de *Littorina saxatilis*).

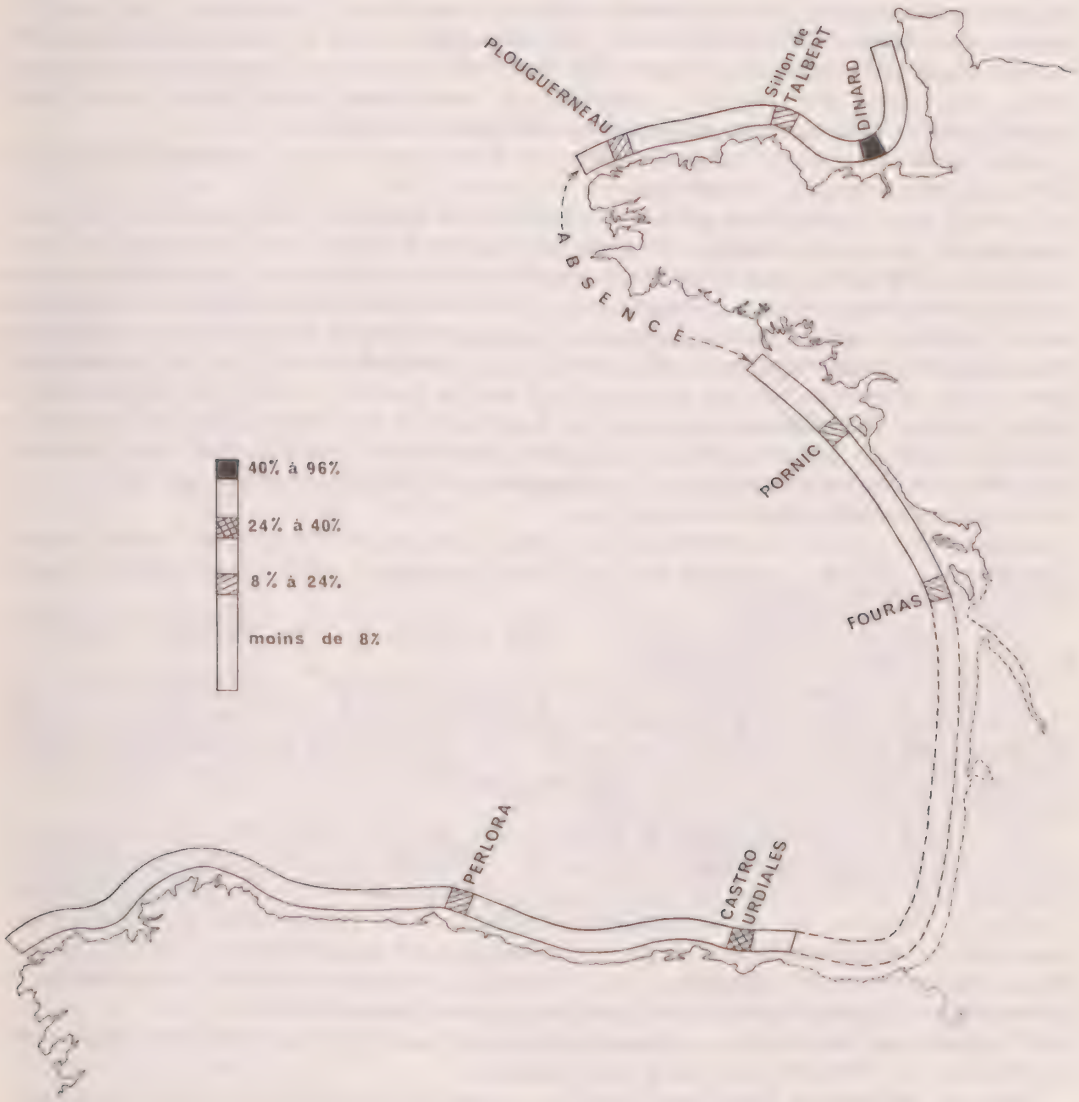

FIG. 2. Carte indiquant le degré d'abondance des individus de la variété *rubescens* relativement aux populations locales de *Littorina saxatilis*. (L'ensemble des stations situées sur la côte continentale s'étendant à l'Est du Cotentin jusqu'à la fin du domaine scandinave appartient à la catégorie "moins de 8%").

regardant la terre. Cela est très gênant pour qui voudrait prendre en considération un rôle d'isolement. On aurait pu penser à ce rôle d'isolement du fait que l'espèce est vivipare, les jeunes à leur sortie de la mer rampent sur la surface voisine sans avoir pu être disséminés, de sorte qu'un îlot ou un piton isolé ne reçoit que bien difficilement des jeunes appartenant à des variétés diverses vivant dans les environs. Pour l'île Harbour il faudrait penser à conjuguer un effet favorable des vagues (pourcentage maximum à la pointe) avec l'effet d'isolement. Nous ne nous engagerons pas dans cette voie.

Nous pouvons penser plus facilement à une action qui se serait située dans l'histoire de ce secteur de Dinard.

Il n'est pas impossible qu'à un moment ou à un autre, pour une cause ou pour une autre, certaines stations de Littorines aient été détruites: que sur leur emplacement les premiers individus arrivés ensuite se soient trouvés appartenir à la variété rouge; et que, étant données les très grandes difficultés de migration pour cette espèce vivipare, ces individus rouges se soient trouvés seuls suffisamment longtemps pour que, au besoin à partir d'un seul couple, une population rouge abondante ait pu se constituer sur la roche. Il faudrait supposer qu'à l'île Harbour la destruction n'ait eu lieu qu'à la pointe Nord de l'île, et que la population rouge qui s'y serait constituée ensuite, se soit étendue vers l'arrière de l'île en ajoutant de nombreux représentants à des populations non-détruites et présentant une variabilité normale.

A quelles causes de destruction pourrait-on penser? A des averses exceptionnelles? Elles n'auraient pas pu être localisées, pour l'île Harbour, sur la seule pointe de ce petit îlot.

Cette pointe est orientée au Nord, donc au large, il n'est donc pas interdit de penser à une tempête exceptionnelle.

Les températures extrêmes peuvent aussi intervenir. Il ne s'agirait pas, sur la pointe Nord, d'un excès de chaleur, mais d'un excès de froid par un vent glacial et persistant venu du Nord et qui aurait donc épargné les populations du revers.

Dans cet ordre d'idées nous voulons rappeler un fait dont l'un de nous a été le témoin (Fischer-Piette, 1964, p 6).

En visitant après les froids de l'hiver 1963 les stations du Cap St. Jacques, de Penlan, de Penestin (Morbihan), de Piriac et Pointe St. Gildas (Loire Atlantique), il constata que les *Littorina saxatilis* avaient disparu de certaines stations (Penlan, Pointe St. Jacques où un seul individu fut trouvé) ou grandement diminuées dans les autres. Mais quelques mois après on y voyait un bon nombre de Littorines, d'une taille souvent normale. Le froid n'avait donc eu pour effet que de faire rétracter et tomber des individus qui étaient remontés ensuite.

Il n'est donc pas très vraisemblable que dans la région de Dinard qui n'est guère plus au Nord, le froid ait pu être letal.

Nous ne percevons donc rien de clair. Quant à une destruction par des huiles lourdes, dont on connaît les exemples récents, on ne peut y faire appel, puisque ces populations rouges homogènes étaient déjà présentes il y a quarante ans donc bien avant qu'on ait vu des grèves se couvrir de mazout.

Variabilité

Nous allons examiner la variabilité de nos échantillons du point de vue de la couleur, de la sculpture et de la taille et nous aurons, ce faisant, à nous demander s'il n'y aurait pas à répartir nos échantillons entre plusieurs variétés.

En ce qui concerne la coloration il y a une assez large variabilité. En général les individus sont d'un rouge peu intense mais ils peuvent aller jusqu'au rouge sang de boeuf. Ceci se rencontre dans la région de Saint-Malo, au Grand Vidé

(n° 117) et à l'île Harbour (n° 119 à 123), stations où ces individus constituent l'essentiel des populations en question. Nous trouvons aussi de tels specimens dans le secteur de l'apparition de l'espèce, au Sud de la zone d'absence du Golfe de Gascogne, à Castro-Urdiales (n° 380). Nous en notons enfin au centre de la côte Nord d'Espagne, à La Franca (n° 415 et 416). Il est à remarquer que c'est dans les stations où se montre le plus fort pourcentage de *rubescens* que la teinte rouge se trouve le plus accentuée.

Ainsi il y a dans ces stations exacerbation locale de cette variété à deux points de vue différents: d'une part celui de son abondance, d'autre part celui de sa réalisation plus complète. Une hypothèse vient à l'esprit: on peut imaginer que dans les secteurs où la majorité des croisements se font entre individus très variés la variété à son état pur est rarissime sinon inexistante. Par contre dans d'autres secteurs, où les croisements se font entre individus déjà fortement marqués par un type précis ce sont les individus qui ne sont pas de ce type qui deviennent rarissimes. Une telle hypothèse serait théoriquement vérifiable par des élevages sélectifs. Sa mise en pratique est difficilement réalisable pour nous qui sommes à Paris.

Nous nous bornerons ici à conclure à la non nécessité d'une dénomination nouvelle pour les specimens du Grand Vidé, de l'île Harbour, de Castro-Urdiales et de La Franca. Ils ne font que traduire une réalisation plus avancée de la variété *rubescens*. Nous sommes hors d'état pour le moment d'aller plus loin dans l'expression, et à plus forte raison l'explication, de ces curieuses constatations.

En ce qui concerne le degré de variabilité de la sculpture des matériaux *rubescens* examinés, on peut noter plusieurs faits: premièrement, l'existence à Altafjord d'une coquille totalement lisse; deuxièmement l'existence, dans un certain nombre de stations, d'échantillons à sculpture très forte constituée de côtes peu nombreuses mais élevées et aigues, c'est le cas dans la région de Dinard - Saint-Malo, à Pordic, à Locquirec, à l'île Hoedic, à Perlora, enfin, dans un site exposé de la Ria del Barquero. Notons que les lots d'échantillons rouges de ces stations peuvent prèsenter un degré plus ou moins important de variabilité de la sculpture, les échantillons cités précédemment en représentant l'aspect extrême. Enfin, dans l'ensemble des autres stations la sculpture est faite d'intermédiaires entre ces deux extrêmes. Cette variété de couleur semble donc ne pas être l'apanage d'une seule variété de sculpture.

On sait que, d'une station à une autre, *Littorina saxatilis* peut varier beaucoup de taille selon les conditions ambiantes. Nous nous sommes posé la question de savoir si, dans chaque station, les échantillons rouges présentaient, relativement à l'ensemble de la population, une différence de taille qu'on puisse exprimer. Nous n'avons rien trouvé de tel.

Examen de quelques facteurs externes

Agitation de l'eau. La variété rouge est-elle limitée à tel ou tel degré d'agitation?

La réponse est négative si l'on prend en considération la totalité des côtes européennes, puisque dans le tableau que nous avons donné par stations certaines de ces stations sont notées comme abritées et parfois même très protégées, d'autres comme exposées (et même, pour un cas, très battue) et que tous les intermédiaires entre ces extrêmes y figurent.

Mais il convient de remarquer que ce n'est qu'aux deux extrémités de la région où la variété peut exister, qu'on la trouve en des points abrités: d'une part dans des fjords de Scandinavie, d'autre part dans la Ria de Camariñas, tandis que dans

le secteur médian, où pourtant les "rivières" bretonnes offriraient toutes possibilités à ce point de vue, des exemplaires rouges ne s'observent pas dans cette situation.

Si nous examinons à l'inverse les régions où les *rubescens* peuvent exister sur les points battus, nous ne constatons pas de limitation (en Scandinavie nous n'avons étudié aucun cas vraiment battu, mais la station n° 4 est relativement battue).

Salinité. *Littorina saxatilis* échappe généralement très largement aux variations de salinité par le fait qu'aux niveaux élevés où elle se trouve ces variations ne se font généralement guère sentir (sinon par la pluie). Ce n'est que dans le fond des estuaires qu'elles sont fortes. La variété rouge ne pénètre pas dans les "rivières" bretonnes, mais elle pénètre dans des fjords ou rias en Norvège et en Espagne. Doit-on donc supposer qu'elle ne tolère pas la dessalure en France et la tolère aux 2 extrémités de son domaine de répartition?

Nous pensons que ce serait une opinion trop absolue. Les fjords norvegiens où nous l'avons vue ne sont pas des estuaires, mais de larges découpures de la côte et les cours d'eau qui débouchent au fond tombent dans une dilatation si vaste que l'eau doit se diluer rapidement. Et en Espagne, ce n'est pas dans les "rios," qui sont les estuaires, mais dans les larges "rias" où débouchent ces "rios," que la variété a été observée.

Nous considérons donc que les conditions d'estuaire ne lui conviennent pas, vraisemblablement pour raison de dessalure, ou peut-être par l'existence d'autres traits des estuaires, tels que la vase en suspension.

Ce qu'on peut dire cependant, c'est que les conditions de "rias" (rias d'Espagne, partie avale des rivières bretonnes telles que la Rance, fjords norvégiens), domaine où se manifeste une légère dessalure, sont supportées par elles aux deux extrémités de son domaine, Galice et Norvège, mais non dans la région médiane (rivières bretonnes).

Cette constatation est très parallèle à celle que nous avons faite ci-dessus au sujet de la possibilité de vivre en milieu abrité.

Ce parallélisme devait assurément être noté, mais ses raisons d'être nous échappent pour le moment et devraient être recherchées.

Temps d'émersion et d'immersion. Les variétés de *Littorina saxatilis* n'ont pas toutes les mêmes exigences vis-à-vis du régime émersion-immersion: la frontière supérieure de leurs habitats n'est pas la même pour toutes.

En ce qui concerne la variété *rubescens*, partout où nous l'avons rencontrée (du moins, partout où nous l'avons rencontrée en abondance suffisante pour juger de la question), elle occupait la totalité de la zone d'habitat de l'espèce.

Lithologie. Il résulte déjà de ce que nous avons dit plus haut que la variété *rubescens*, tout en ayant été trouvée presqu'uniquement sur des terrains durs, ne craint cependant pas les grèves tendres, puisque nous l'avons trouvée sur la côte basse de "La Fumée" à Fouras.

Rôle de la topographie de détail du substratum. La variété *rubescens* nous semble assez indifférente au genre de grève qui peut la porter. Elle peut vivre sur une falaise abrupte (exemple: Flamanville, n° 51), en couloir (exemple: Flanc Est de l'île Harbour, n° 120), sur de petits groupes rocheux (exemple: Carolles, n° 56), sur des gros blocs posés sur sable (Kersaint, n° 186), ou parmi les pierrailles (exemple: Stallogargo, n° 11).

L'indifférence n'est toutefois peut-être pas totale, car, à Castro-Urdiales (n° 380) la variété n'existe que dans un champ de cailloux et non dans les autres types d'habitat où se voient en cette station des *Littorina saxatilis*. Or, Castro-

Urdiales est l'une des rares stations où le pourcentage de cette variété soit important puisqu'il est de 12%. Il doit bien y avoir une cause à cette localisation des *rubescens* dans le seul champ de cailloux qui sur cette grève existent à leur niveau d'habitat, d'autant plus que le fait s'est révélé constant au cours des 5 visites, réparties sur 10 ans, que nous y avons faites. On pourrait par exemple supposer que les jeunes de la variété *rubescens* soient moins résistants à la turbulence que ceux d'autres variétés.

Mais on pourrait aussi supposer que les exemplaires rouges soient plus visibles que d'autres pour les oiseaux de mer, qui n'auraient pas d'obstacle à les saisir sur une paroi découverte tandis que dans un champ de cailloux de nombreux individus leur échapperaient.

CONCLUSIONS

Nous nous sommes efforcés dans cette note d'établir la distribution de la variété *rubescens* de *Littorina saxatilis*.

Il était utile de faire connaître ces faits qui contribuent à nos connaissances sur l'écologie de la variation chez *Littorina saxatilis*. Mais il faut reconnaître qu'ils n'éclairent guère l'ensemble des problèmes concernant cette espèce et que même pour la seule variété *rubescens* les explications de ces faits n'ont pas pu être saisies par nous. Or déjà nos études antérieures ne nous avaient donné qu'un bien faible nombre d'explications en égard aux problèmes qui au contraire se sont posés en foule et dont certains sont d'une incroyable complexité. Or le nombre des documents que nous avons jusqu'ici présenté dans nos diverses publications, si grand qu'il soit, est nettement inférieur à celui que contiennent encore nos carnets de notes (et les tableaux d'analyse de nos récoltes). Et il nous faut encore fournir une somme énorme de travail pour pouvoir les exprimer convenablement.

Certes *Littorina saxatilis* est une des espèces des plus variables et d'autres espèces ont fourni ou fourniront un travail moins malaisé.

Mais nous croyons pouvoir et devoir dire ce qui suit.

Nous pensons qu'une des tâches les plus importantes qui appellent actuellement les efforts des zoologistes, est l'étude de la variation intra-spécifique. L'étude de l'espèce a tellement absorbé, et à bon droit, des générations de naturalistes, que l'étude de la variation intra-spécifique n'a connu qu'un bien plus faible développement. Or elle est tout aussi vaste, peut-être bien plus, et, à notre avis, tout aussi nécessaire pour nous préparer à comprendre ce qu'est la nature et en quoi a pu consister l'évolution.

Quoi qu'il en soit, voici, pour la variété *rubescens* de *Littorina saxatilis*, le résumé des faits relatés dans le présent travail.

On aurait pu penser que, dans toutes les stations de *Littorina saxatilis*, ou tout au moins dans toutes celles qui ne sont pas dans des conditions extrêmes telles qu'en eau saumâtre, ou très avancées en mer, etc., les *rubescens* pouvaient exister et être représentées dans une proportion peu variable. Il n'en est rien. D'abord elles font défaut de l'angle de la Galice au détroit de Gibraltar, ce qui montre peut-être qu'elle ne supporte pas des conditions trop méridionales. De plus, sur le reste des côtes européennes, il y a des régions où elle est introuvable: du Cap Gris-Nez (extrémité orientale de la Manche) à Flamanville (côte Ouest du Cotentin) et de Kersaint (angle de la Manche et de l'Atlantique) à Quiberon. Enfin, dans les autres régions, celles où on peut la rencontrer, elle ne se présente pas dans toutes les stations, loin de là, et lorsqu'elle est présente son pourcentage est très variable, de moins de 1% à 96%. Le plus souvent il est inférieur ou égal

à 8%, et ne dépasse ce chiffre que dans un très petit nombre de secteurs très étroits et très distants les uns des autres. Comme ces quelques secteurs sont dans des conditions qui ne présentent pas beaucoup d'analogies, nous ne connaissons pas les raisons qui y autorisent des pourcentages plus élevés qu'ailleurs. Simplement, dans le cas de très forts pourcentages, nous nous demandons s'ils ne sont pas venus à la suite d'un dépeuplement total par des causes externes temporairement extrêmes; mais même cette dernière supposition est malaisée du fait qu'en un tel cas, récemment observé, de dépeuplement brutal (par un froid exceptionnel), les individus s'étaient rétractés et avaient disparu en tombant mais que beaucoup étaient remontés ensuite.

La variété est indifférente à l'agitation de l'eau, on la trouve depuis des localités bien abritées jusqu'à des localités très exposées, toutefois ce n'est qu'aux deux extrémités de son domaine d'habitat (Scandinavie et Galice) qu'elle va jusque dans des points abrités.

Elle ne semble pas pouvoir supporter de forte dessalure, du moins ne l'avons nous jamais trouvé dans de telles conditions.

Dans le sens vertical sa répartition ne subit pas les limitations qu'on peut constater chez quelques autres variétés: elle peut exister sur toute la hauteur de la zone où l'existence de *Littorina saxatilis* est possible.

C'est presque toujours sur des côtes résistantes qu'on la trouve mais elle peut exister aussi sur un rivage peu résistant.

Elle peut vivre dans des types topographiques d'habitat très divers, falaise abrupte, grèves moins inclinées ou peu inclinées, couloirs, groupes rocheux isolés, gros blocs sur sable, champs de pierrailles. En une station (Castro-Urdiales) elle est limitée au champ de pierrailles, tandis que d'autres variétés s'étendent davantage (raison: abri contre les vagues? Abri contre les oiseaux de mer?).

Ces caractéristiques de la distribution de la variété *rubescens* nous donneront une base de comparaisons lorsque nous publierons un travail plus général.

Nous pouvons d'ailleurs tenter de situer certains de ces résultats par rapport à certains de ceux qu'ont donnés nos essais antérieurs, ou inversement. Cela va nous permettre d'élargir certaines questions.

Nous avions montré qu'il y a des variétés qui peuvent se trouver localisees en des points très éloignés les uns des autres et, sans raison apparente, faire totalement défaut entre eux. Ce phénomène peut maintenant nous apparaître comme un cas extrême, par réduction de l'étendue des régions de présence, de ce que nous montrent les *rubescens* avec leurs régions de présence alternant avec des régions d'absence. Dans un cas comme dans l'autre, du fait que nous ne voyons pas facilement d'explication du côté des conditons ambiantes, on peut penser à ramener cela à des questions génétiques. Cela serait en effet assez satisfaisant dans le cas de variété tout-à-fait localisées séparées par des lacunes immenses. Dans le cas des *rubescens* il resterait à comprendre pourquoi des types qui se manifestent sans grande difficulté dans de vastes régions, ne parviennent pas à se manifester en d'autres vastes régions alternant avec les premières: mais cela ne change pas le fond de la question, qui, à nos yeux, doit avoir une grande importance dans l'étude de la variation intra-spécifique.

Prenons maintenant le fait que les *rubescens*, dont le pourcentage est généralement faible, peuvent en quelques stations, être bien représentées, et parfois en populations presqu'exclusives. Nous avons cherché, sans grand succès, si cela ne pouvait pas s'expliquer par des facteurs locaux ou des évènements locaux. Or en nous reportant à des constatations contenues dans nos travaux antérieurs nous pouvons là aussi élargir le débat. Reprenons en considération les variétés pouvant

exister très localement dans des localités très distantes, dont nous venons de parler. Parmi ces localités il en est où ces variétés sont exclusives ou hautement dominantes par exemple les *nojensis* à Noja et Punta Muiños, les *sellensis* à Ribadesella, les *zonaria* à bande brun chocolat à la Maison perdue, à l'île Hoedic, etc. ...

En fait, pour toutes ces localités à population pratiquement homogène, se pose le problème que nous nous sommes posé pour le Grand Vidé (St. Lunaire) et l'île Harbour à propos de la variété *rubescens*. C'est donc un problème étendu et intéressant, et nous devons d'ailleurs dire que pour le choix de la question à traiter dans cette contribution n° IX nous avons hésité entre le sujet concernant la répartition des *rubescens* et un sujet traitant de la distribution, le long des côtes, des stations à populations homogènes pour essayer de savoir ce qui pouvait provoquer des isolements de caractères.

En outre il nous paraît difficile de penser que la question de l'isolement, en certaines localités, de caractères qui ailleurs sont mélangés aux autres et présentent avec eux tous les intermédiaires, puisse ne pas avoir de connexions avec une autre question, que nous avons exprimée comme un "difficile problème" au sujet des *lutea* et des *lineata* dans les rias de Galice (Fischer-Piette, Gaillard & James, 1964b, p 132). Nous avons montré là qu'il pouvait y avoir au voisinage l'une de l'autre, sans différences apparentes de conditions externes, une station peuplée uniquement de ces deux variétés sans qu'il y ait pratiquement d'intermédiaires entre elles, et une station peuplée de ces deux mêmes variétés mais avec tous les intermédiaires entre elles: comme si dans la première, contrairement à la seconde, il y avait une barrière génétique, pouvant faire penser à une différence spécifique, tandis qu'il n'y en aurait pas dans la seconde où les deux variétés appartiennent incontestablement à une même espèce. Encore, dans son dernier travail, James (1968, p 152) parle des faits de cet ordre qui se présentent aussi en Grande-Bretagne. Nous avons le sentiment que tout cela est lié en une seule et même très vaste question, qui pourrait fort bien se révéler être très importante.

Nous ne sommes pas encore parvenus à intituler cette question, ce qui prouve que nous ne la concevons pas encore bien, puisque ce qui se conçoit bien s'énonce clairement. Mais son existence augmente notre conviction qu'il est très désirable que de plus en plus, des zoologistes développent l'étude de la variation intraspécifique en y appliquant à la fois leur mentalité de systématicien et celle d'écologiste.

RESUME

Dans l'étude infiniment complexe de la variation de *Littorina saxatilis* où jusqu'ici nous nous sommes essayés sur certains facteurs ou certaines localités, nous nous essayons cette fois sur une variété donnée recherchée sur 9.000 km de côtes, de la frontière soviétique au détroit de Gibraltar: la variété *rubescens*, dont nous donnons la distribution à titre d'exemple et de base de comparaison.

Elle manque sur toute la côte Ouest ibérique, peut-être trop méridionale pour elle. Son aire de répartition va donc de l'Océan glacial à l'angle de la Galice, mais dans cette aire de répartition il y a de vastes secteurs d'où elle est absente pour des raisons qui nous échappent: du Gris-Nez au Cap de la Hague et de la sortie de la Manche à Quiberon. Dans les régions restantes il y a moins de stations où sa présence se constate, que de stations où elle n'a pas été trouvée. En particulier elle fait défaut dans les milieux dessalés ou très abrités sauf aux

deux extrémités de son aire de répartition. Là où elle existe, son abondance, généralement faible (moins de 10%), est plus forte en de rares stations irrégulièrement réparties, et peut approcher 100% en quelques-unes. Ces irrégularités de répartition et d'abondance posaient des problèmes dont l'existence nous semble devoir permettre de mieux embrasser certains de ceux qu'avaient révélés nos précédentes publications. Il reste énormément à faire dans ces recherches qui sont certainement prometteuses.

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A NEW SPECIES OF THE GENUS *CYCLOTEUTHIS* (CEPHALOPODA: OEGOPSIDA)

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A very interesting squid of the rare genus *Cycloteuthis* was captured in the Central Indian Ocean during the 35th cruise of the R/V "VITYAZ," in which the present author took part. Until lately this genus was known but from 1 specimen taken in 1912 in the North Atlantic, near the Isle of Madeira (30° 45' N, 25° 47' W). The French teuthologist, L. Joubin described this previous specimen in 1919 as a new genus and species *C. sirventi*. This species has not been encountered since that time. Now, after 50 years, a representative of this genus is encountered for the 2nd time, but from quite a different part of the world. A thorough comparison of this most recent specimen with the description and figures reported by Joubin 1919, 1924) has shown that besides their different sizes (the mantle length of *C. sirventi* was 49 mm, while that of the Indian Ocean specimen was 196 mm), a number of peculiar features distinguish the Indian squid from *C. sirventi*, thus indicating that it is a new species.

Cycloteuthis belongs to the Family Cycloteuthidae (=Parateuthidae) whose characters coincide with those of its single genus.

Genus *Cycloteuthis*

The diagnosis of the genus *Cycloteuthis* is expanded here, to take into consideration characters of the 2nd species, described in the section to follow. The mantle is conical with the long tapering posterior end which projects beyond the large rounded fins. The funnel cartilage has an irregular shape, with a fossa surrounded by a swell of moderate height. The mantle cartilage is shaped like a double-humped rib: the front part is more prominent while the back one is declivous. The tentacles are stout with large clubs, which are furnished with adherent suckers and pads at their bases. These basal suckers and pads vary in number from 3-5 in *C. sirventi* to 7 in *C. akimushkini*. The suckers of the club are arranged in 4 rows. Their chitinous rings are encircled with minute teeth. The gladius with the wide vane runs along 2/3 of its length. The edges of the vane gradually turn ventrally, to fuse completely into a posterior hollow horn. The gladius terminates as a small single chitinous conus.

The buccal membrane is 7-pointed. The ventral arms are connected on the ventral surface. There is a large light organ between the gills (in *Cycloteuthis sirventi;* not determined for *C. akimushkini*), and a wreath of small rounded orange photophores around the eye.

Cycloteuthis akimushkini, new species

Holotype: mantle length 196 mm, VITYAZ Sta. 5207, 9° 57' S, 91° 31' E, Isaacs Kidd trawl, depth 100-120 m, 29 August 1962. The Holotype is located in the Institute of Oceanology of the USSR Academy of Sciences.

Description. The body has an extremely peculiar shape (Fig. 1a). The mantle is shaped like a funnel with a long, narrow point, and it is unusually broad anteriorly. It tapers sharply posteriorly into a long, narrow tail, which projects 4 cm beyond the fins. The head is significantly narrower than the mantle opening and is deeply pulled into the mantle cavity, forming a broad mantle margin like

a high collar around the lower part of the head, leaving the eyes and terminal funnel section free. Because of the position of the head, the mantle-locking cartilages are deeply embedded - disposed on the inner mantle wall at 20 mm from its edge. Similarly, the anterior edge of the gladius is within 20 mm of the anterior mantle margin. Such an arrangement of the gladius and cartilages is unusual, and so far has not been found in any other squid. The mantle walls are rather compact. The anterior dorsal mantle margin is slightly projected forward in a rounded angle. A strongly pronounced muscular ridge runs longitudinally on the dorsal surface of the mantle. It is 3 mm high and 7 mm wide. Anteriorly, this ridge is undivided for a distance of 20 mm, whereupon it bifurcates, and the 2 crests, separated by a deep groove, run parallel to the base of the fins.

The fins are large, rounded and fused together in the median line. Their length is about 1/2 of that of the mantle; their width is somewhat greater. When the skin is peeled off the fins, well-marked parallel muscular fibres are revealed, which cross transversely the longitudinal axis of the body.

The funnel is fairly large, but almost entirely hidden by the anterior mantle margin, with only its terminal part protruding outward.

The funnel cartilage is irregularly elongated with a fossa in its anterior part and a shallow longitudinal groove behind (Fig. 1b). The cartilage margin is formed of a ridge and adjoining skin rim. The corresponding mantle cartilage is on the inner surface of the mantle, within 20 mm from the mantle edge. It consists of 2 ridges which are unequal in height. The highest frontal one, shaped like a human nose, overhangs the posterior, less protruding crest (Fig. 1c).

The nuchal cartilage presents a shallow longitudinal groove with 2 moderate side ribs. The corresponding mantle member is a fairly indistinct ridge.

The funnel organ is strongly developed. It consists of a dorsal lobe, shaped like an inverted V with 2 oval ventral pads (Fig. 1d). From the bases of both branches of the dorsal lobes are highly raised scalloped ridges made up of a membranous tissue. At their point of fusion a 3rd odd ridge is found, which is not connected with the former 2. The above members of the funnel organ are rather voluminous, so as to fill up most of the funnel cavity.

The tissues of the head and arms are soft and fleshy. The eyes are large. The arms, stout at their bases, become gradually more slender distally. Unfortunately, it was not possible to accurately measure the length of the arms, since all of them had their tips torn away. The relative lengths of the ventral arms are rather significant, reaching about 70% of the mantle length.

The basal suckers are in 2 rows, but at the distal 1/3 of the arm length they appear to be arranged in 1 sinuous series. On the outside of the suckers, the oral surface of each arm is bordered for its entire length by a moderately high skin membrane with muscular supports originating at the bases of the suckers. The largest suckers (3 mm in diameter) are on the 2nd and 3rd pairs of arms, while the smallest ones (1.3 mm) are on the 4th pair. The suckers are rounded, with dark chitinous rings on the distal margin equipped with poorly differentiated short teeth, varying in number from 6 to 8.

The tentacles are long, somewhat longer than the mantle. The tentacular stalks are stout and compact, laterally flattened at their bases, becoming tetrahedral

FIG. 1. *Cycloteuthis akimushkini* sp. nov.; a, dorsal view of the squid; b, funnel cartilage; c, mantle cartilage; d, funnel organ; e, arm sucker; e_1, arm sucker, lateral view; f, sucker of basal part of club; g, radular teeth; h, mandibles.

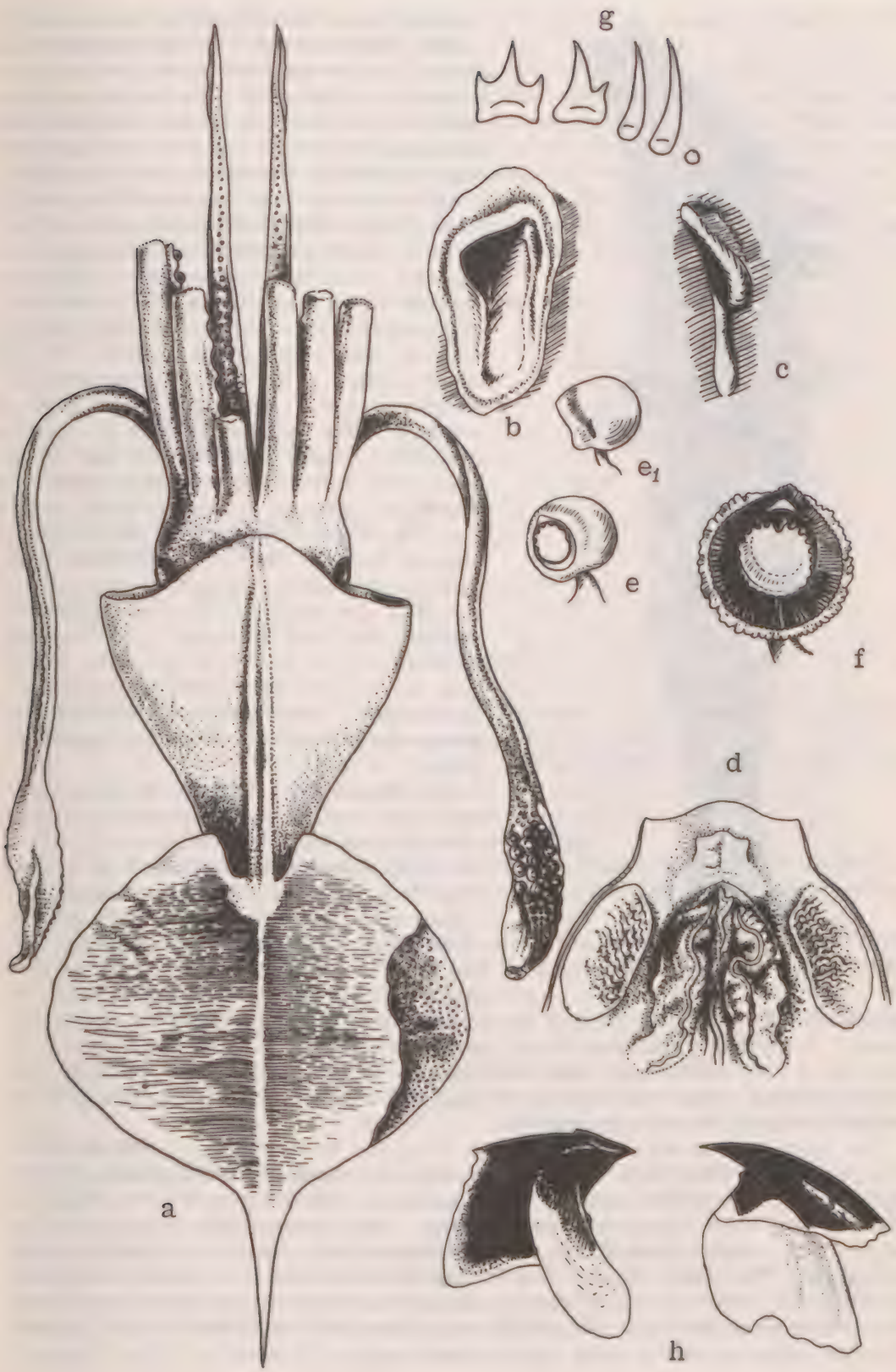
g
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FIG. 2. Club of tentacle (photograph).

further along. A light-coloured fold of moderate height extends for most of the stalk length on its outer face, and disappears at the base of the club. The club is well expanded. At the base of the club there are well defined knobs and adhesive suckers, which are equal in number on both tentacles, i.e., there are 7 suckers and 7 knobs on each (Fig. 2). The club is bordered by a protective membrane, which goes to the end of the club on its ventral margin but only midway on its dorsal margin. The membrane is crossed by transverse muscular supports running from bases of the suckers. On the outer surface of the club there is a powerful swimming keel. The club bears 4 rows of suckers. The largest of them (4.3 mm in diameter) occupy the proximal half of the club. These suckers are on stout peduncles which are inclined distally, with the result that the sucker body itself is more distally located than the base of its peduncle. The farther the suckers are from the base of the club, the smaller they become, and the shorter are their pedicels. The smallest suckers are at the tip of the club, where they form a corona around the naked terminal area. These suckers, like the locking ones, are equipped with smooth chitinous rings.

The larger club suckers are armed with dark-coloured, almost black chitinous rings with high walls; the distal part of the ring projects outward in the shape of a beak (Fig. 1f). The ring edge is swollen and furnished over the entire circuit with coarse, blunt teeth, 20-24 in total number. The teeth of the distal portion are somewhat larger. The 1st, inner chitinous ring is surrounded by a 2nd one found on the flattened sucker edge, consisting of narrow, radial, dark-brown chitinous bands, packed so closely together as to appear at first as a continuous ring. The outer margin of this ring is finely toothed. The tissue coating every sucker cup is equipped with minute folds, which give the sucker margin a fringed appearance.

The gladius originates within 20 mm from the mantle margin. The rachis is sharply pointed anteriorly. The vane area runs along 2 3 of the gladius length. Its lateral edges turn ventrally; they touch in the posterior area of the fins, and distally they fuse, forming a hollow cone. The terminal part of the gladius is shaped like a minute (3 mm), thin, single chitinous conus, slightly curved ventrally at the end. The radula bears 7 longitudinal rows of teeth. The central teeth have 2 additional cusps on either side of the median cusp; the 1st lateral teeth have only 1 side cusp (Fig. 1g). The lateral wall of the lower mandible is equipped with a rather indistinct gentle ridge running fairly parallel to the crest. The wings are

translucent, cartilaginous. The mandible is dark brown except for a light-coloured rim bordering the lateral wall (Fig. 1h).

No traces of photophores or light organs were found on the surface of the body. Minute (up to 1 mm in diameter), round, orange-coloured photophores were found in the eyelid tissues, which form a corona around the eye opening. Their exact number was difficult to determine because of the very poor condition of the eye. Fifteen photophores could still be identified around the left eye. Nothing could be determined about a light organ similar to the one found in the mantle cavity of *Cycloteuthis sirventi*, because the squid described in the present paper was substantially damaged when captured, which resulted in most of the viscera being lost.

TABLE 1. Comparative measurements of *Cycloteuthis sirventi* and *C. akimushkini*

Feature		*C. sirventi*	*C. akimushkini*
Mantle length in mm		49	196
Fin length / mantle length	(%)	61.2	51.0
Fin width / mantle length	(%)	98.0	53.5
Arms IV length / mantle length	(%)	83.0	70.0
Tentacle length / mantle length	(%)	179.0	107.0
Club length / mantle length	(%)	34.0	26.0

DISCUSSION

Cycloteuthis akimushkini is without doubt related to *C. sirventi*, but it is easily distinguished from the latter by possessing the following features:

1. An unusual shaped body with a broad anterior mantle margin, which covers the lower portion of the head and nearly the entire funnel.
2. The gladius and funnel cartilages are deeply buried.
3. A strongly defined muscular dorsal ridge.
4. Somewhat different body proportions: the fins in *C. akimushkini* are relatively narrower and shorter (relative to the mantle length) than those of *C. sirventi*.
5. The numbers of suckers and pads at the base of the club are different, i.e., 7 suckers and 7 pads in *C. akimushkini*, while *C. sirventi* bears but 3 suckers and 5 pads on one tentacle and an inverse number on the other one.
6. The radula in *C. akimushkini* bears 1 additional cusp on the 1st lateral tooth, while in *C. sirventi* there are 2 such cusps.
7. Somewhat different structure of the funnel cartilage.

In recognition of the very important works by the well-known Russian teutholo-gist, I. I. Akimushkin, the author has given the new species the specific name *akimushkini*.

When Joubin studied the squid which he subsequently described as *Cycloteuthis sirventi*, he was somewhat startled by an intricate combination of characters, which did not allow him to place his new species in any of the several families recognized at that time. Consequently, Joubin (1919) erected a new family Para-teuthidae, which included (without sufficient grounds) the genus *Lycoteuthis*. Some authors did not recognize this new family and placed the genus *Cycloteuthis* in the family Onychoteuthidae (e.g., see Thiele, 1934). Other workers treated the family

Parateuthidae as a catch-all taxonomic category which united several monotypic genera which did not possess any typical features in common (e.g., see Clarke, 1966).

It is my belief that the genus *Cycloteuthis* cannot be attributed to any definite family known, even though this genus does contain certain characters similar to those of several other groups. For example, the way in which the arms are attached and the structure (but not the situation) of the funnel and mantle-locking cartilages are common to both the family Chiroteuthidae and the genus *Cycloteuthis*. The genera *Cycloteuthis* and *Mastigoteuthis* have a somewhat similarly shaped gladius. On the other hand, the shape and structure of the club, as well as the condition of the pads and the fixing suckers being developed on the tentacular stalks, recalls the family Histioteuthidae.

A thorough comparison of the systematic features of the 2 known species of the genus *Cycloteuthis* has led me to agree with Joubin that this genus should be placed in a separate family.

Both specimens of the genus *Cycloteuthis* have been taken at a depth somewhat shallower than 500 m. A large fin, a well developed funnel, and muscular tentacles with stout clubs indicate that these animals are good swimmers, i.e., active pelagic dwellers.

I wish to thank E. I. Mussayeva, who caught the new squid named here, and V. M. Gudkov, for the execution of the illustrations.

ABSTRACT

A new species of a rarely encountered genus *Cycloteuthis* is described on the basis of a specimen taken in the central part of the Indian Ocean by the research vessel "VITYAZ." The new species, *C. akimushkini*, possesses a number of quite peculiar features. Only a single species of this genus, *C. sirventi* Joubin 1919, was previously known; it was described from only 1 specimen captured in the North Atlantic. This description of a 2nd species expands the diagnosis of the genus.

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MOLLUSCAN ORGAN CULTURE[1]

C. J. Bayne

INTRODUCTION

Organ culture can be defined as the culture of whole organs or fragments or rudiments of organs, outside the host body, in such a way that the experimental object assimilates nutrients from the medium and maintains its integrity for a period exceeding that taken to exhaust at least some of its own metabolic reserves; it should exhibit some activity such as functioning, differenciation or growth (Sengel, 1964).

The purpose of the present paper is to review the present status of organ culture work with molluscs, and to examine the background upon which present methods have been developed.

HISTORICAL BACKGROUND

The historical background of cultivation of organs is related, especially in the early days, to tissue and cell culture.

The Frenchman Jolly in 1903 published a paper which was the first to report observations on animal cell growth *in vitro*. The foundation of *in vitro* culture in America was laid 4 years later when Harrison (1907) published his paper on the culture of nerve fibres. Not until 1915 in America did Goldschmidt demonstrate for the first time successful *cultivation*, rather than just maintenance, of invertebrate cells *in vitro;* his interest, however, was in insects. This technique was not applied to molluscs until the 1920's when Zweibaum (1925) kept gill filaments of *Anodonta* in a medium which included peptone, and observed mitoses for up to 7, or in some cases 10, days in culture. Gatenby in 1931, and later (1933, 1934 (with Hill)), attempted to culture pieces of various tissues from *Helix aspersa*. At about the same time Bohuslav (1934) and Janda & Bohuslav (1934) in Czechoslovakia published the results of similar work on *H. pomatia* and *A. cygnaea*. These authors, however, and several who have followed (Buchsbaum, 1937; Flandre & Vago, 1963; Burch & Cuadros, 1965) were interested mainly in obtaining outgrowths from the tissue fragments; that is, their interest lay more in the field of cell and tissue culture than in organ culture. As has been stated by Benex (1966), "work in which attempts are made to obtain cell lines from molluscan explants without being preoccupied with the source of the explant . . . have different aims and use different methods . . ." from those we are primarily concerned with in this discussion.

In 1933 another paper on *Helix pomatia* (Köničcek, 1933) reported an unsuccessful attempt to grow whole hearts in culture. During the 1940's there was only one report of organ culture with molluscs. This was by Bevelander & Martin (1949) and described the culture in molluscan hemolymph of mantle tissue from marine molluscs. Carriker (1946), to facilitate investigations on the functioning of the alimentary system of *Lymnaea stagnalis*, devised a physiological saline in which tissues could be kept alive for periods in excess of 60 hours. Since then a large

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number of neurophysiological and pharmacological investigations have been reported in which use has been made of physiological salt solutions (Jaeger, 1962; Roach, 1966; Frontali, Williams & Welsh, 1967; Lawrence & Lawrence, 1967; Leenders, 1967; Lai & Agarwal, 1968; Mirolli, 1968; Kerkut, Rick & Huggins, 1969; see also Lockwood, 1961, for a useful review). One aim of these investigations is the maintenance of nervous and/or muscular activity in the tissues or organs long enough to permit short term experiments. The science of organ culture can, however, benefit from such work, as the success or failure of salines can indicate physiological requirements of tissues and organs.

During the 1940's the Frenchman Thomas (1948) was publishing the results of work on amphibian organ culture and the culture of echinoderm organelles. The significance of this is that Thomas's work has been the main influence behind some of the modern workers in molluscan organ culture (Benex, 1966). Two other authors were to prove very influential on modern workers; they were Wolff & Haffen (1952) who developed a simple two-phase technique for the culture of bird embryos.

These investigators did not influence malacologists until the 1960's. In the meantime in France molluscan organ culture was beginning to receive serious attention. This may be related to the fact that in the early 1950's excellent work was being carried out in that country using operative techniques on gastropods (see Laviolette, 1950, 1951, 1954a, b). In 1954, Jullien, Cardot & Rerat published the results of their work on attempts to prolong the survival of *Helix pomatia* hearts *in vitro*, using low temperatures and a simple salt solution. In the following year Binet, et al. (1955) assessed the effects of glucosamine and many other compounds added separately to the saline, and reported the survival of active hearts for more than a month. In America, Friedl (1958), in an unpublished thesis, reported attempts to cultivate portions of *Lymnaea stagnalis*. Thus, until the present decade there were about 16 papers in which culture methods were described for molluscan tissues, or organs, and in less than half of these were the authors primarily interested in organ culture. None of them claimed any real success. The reasons for this are worth considering.

Firstly, the methods which had been described were worked out for vertebrate tissues. The control of the internal environment may be less well developed in invertebrates and conditions such as pH, osmotic strength, ionic composition, nutrient and excretory content differ significantly from vertebrate body fluids. Secondly, a large degree of ignorance of invertebrate biochemistry, and the danger of fungal and bacterial infection, together slowed the progress of organ culture studies (Sengel, 1964). Finally the small size of many invertebrates and the small volumes of hemolymph available from them probably also complicated and adversely influenced attempts to culture invertebrate tissues and organs.

During the 1960's 2 laboratories in the United States have published the results of culture work with snails; though this work has primarily been concerned with tissue culture, several aspects of it are of interest to our discussion.

Chernin (1963, 1964) at Harvard, as well as Burch & Cuadros (1965) and Burch (1968) at the University of Michigan, used *Biomphalaria glabrata*, the intermediate host of human schistosomiasis, as their experimental animal, although duplicate experiments were done by Burch & Cuadros with *Helix pomatia* and *Pomatiopsis lapidaria*. In both laboratories outgrowth of cells from the explants was observed. This may be related in part to the incorporation into the media of calf fetal extracts, a preparation widely used for obtaining cell growth in culture. In Chernin's work (1963), when the snail hearts were not trypsinized prior to being explanted there was less cell migration, and cell migration did not

occur (1964) when fragments of ovotestis and digestive gland were kept in either a basic salt solution or a complex medium.

Most of the media used in these experiments incorporated a basic salt solution, antibiotics and various chemically undefined complex organic additives. A comparison of Chernin's and Burch's results reveals several interesting variations. For example, Chernin's work with hearts and with fragments of gonads and digestive glands was carried out at pH 7.3-7.5, whereas Burch & Cuadros found that gonads did well at pH 7.0 and foot-muscle tissues did well at pH 8.5. Burch & Cuadros experimented with temperatures and found that 15° C was optimal for their cultures. Chernin however kept his cultures at 26-28° C without ill effect. Another interesting difference, but one which might be expected due to the different tissues involved, is that Chernin did not observe cell divisions in the heart, but Burch (1968) using (amongst others) Chernin's medium, reported that there were ". . . an adequate number of mitoses . . ." in the gonad for chromosome studies. With reference to organ cultures, however, Parker (1961) has this to say ". . . very active mitosis should not be encouraged in organ culture, for 2 reasons: First, conditions that favor active mitosis also favor cell migration; and cell migration must always be suppressed in organ culture. Secondly, because organ cultures have no circulation, they must feed, respire and excrete by diffusion; for this reason they must not be allowed to become too large. If there is too much growth, the interior will become necrotic, and this is likely to lead to poisoning of the superficial cells and death of the explant." The differences referred to above, together with other data not mentioned specifically, jointly indicate that our knowledge of the actual requirements of invertebrate tissues is still very limited. However, Burch & Cuadros (1965) report that factors found to be important in cultivating snail tissues were sterility, proper antibiotic mixture, temperature, pH and addition of "snail extract." To this list could be added ionic balance, osmotic concentration and provision of suitable nutrients (Vianey-Liaud & Lancastre, 1968). Various tissues survive better at different pHs. This factor, among others, is one that dictates the need for different media for probably every species. Also, the seasonal and life cycle changes in snail hemolymph composition indicate that the same tissue from the same species may require different media depending on the time of the experiments. In fact Ripplinger & Joly (1961) have found that the heart of *Helix pomatia* varies in its sensitivity to different ions depending on the season of collection. This may be related to as yet undiscovered hormones. Also, Benex (1966) mentioned that solutions suitable for culture of *Helix* hearts in one season may actually be toxic in another season.

It is tempting for the novice to feel that he must design a medium which will provide the organs with as nearly as possible precisely what they require. It is probably true, however, that in order to progress toward this goal the only approach to follow is to find a medium, any medium, which "works" - that is, insures survival. From there one may proceed to investigate whichever problems are of interest. The use of chemically defined media is an ideal as yet seldom achieved (Hollande, 1968; Guyard, 1969).

RECENT RESEARCH WITH MOLLUSCAN ORGAN CULTURE

Between 1960 and 1969 at least 30 papers were published dealing expressly with organ culture of molluscs. All of this work was done in France and published in French.

In these recent investigations 2 lines of methodology have been developed. The

first - using a single-phase liquid medium - is based on the work of Thomas (1948), and the second - using a two-phase gel and liquid system - is based on the work of Wolff & Haffen (1952). The majority of investigators have adopted the latter. In addition, Flandre & Vago (1963) have themselves developed some new culture techniques, but with interest mostly in tissue culture.

Cephalopod, bivalve and, predominantly, gastropod organs have been studied. In reviewing this work it is convenient to deal first with those papers which discuss *survival* of organs *in vitro*, and then to review those papers in which organ culture has been used to study *endocrinology* and other physiological phenomena.

The most significant work in the field of organ survival and the design of culture media is that of Benex (1964a, b; 1966; 1967a, b). Using tentacles of *Biomphalaria glabrata* (because (1) they are the preferred site of entry of schistosome miracidia, (2) they have ciliated epithelia [a useful criterion of survival], and (3) they are easy to remove), Benex (1966) has assessed the effects of practically all the components in her media. She has been the main exponent of the one-phase system, following the work of Thomas (1948). She has, however, made a general review of previous organ culture work (Benex, 1966).

In her own work Benex sterilized the surfaces of the snails by submersion for 10 minutes in a saturated, filtered, aqueous solution of Furadoine (nitro-5-furfurylidine-2-amino-hydantoine) [Chernin (1963) showed that streptomycin, a fungal-derivative antibiotic, adversely affected growth of *Biomphalaria glabrata*.] In her research Benex tried a whole series of antibiotics and antimycotics in her culture media, and those found to be most effective were colimycine and tetracycline. Whereas some earlier tissue culturists (Gatenby & Hill, 1934) had found that absolute sterility was unnecessary, Benex and other modern researchers emphasize that success requires that all precautions be taken to ensure sterility. No quantitative data are, however, available as proof of this.

With reference to nutritive requirements, Benex (1966) reports that survival of *Biomphalaria glabrata* tentacles is 8-10 days in saline alone, but may extend to 4 weeks in the complete medium. It has been stated (Ripplinger & Joly, 1961) that the best medium for hearts would be hemolymph. However, it is as well to remember that hemolymph in addition to being the "source" is also the "sink" for metabolites in the body (Jones, 1966). Benex changed the medium daily or every 2 days, but again it is not clear how necessary this is, and the need no doubt varies with the exact conditions of the experiment; 8 days has been found sufficient in certain circumstances (Guyard & Gomot, 1964). Benex favours the use of test tubes above the use of petri dishes as the smaller surface area reduces the likelihood of bicarbonate decomposition and alterations of pH.

The addition of embryo extract (either chicken or beef) has become almost traditional for tissue culture media; these fluids apparently contain elements which encourage cell growth. Sengel (1961) cultured gill filaments and intestinal diverticulae of the bivalve *Barnea candida* in media containing, and in media lacking, chick embryo extract. Without this additive the organs maintained their integrity better, as less cells grew out of the explant. Ripplinger & Joly (1961) using *Helix* hearts, found that both oxygen and ionic composition were important; the survival of the heart was enhanced if nerve extract, which contains an active amino compound, was added to the medium. The level of this substance in nerve extract and indeed the receptability of the heart varied with the seasons. Hemolymph does not contain this active amino substance; hemolymph dialysate does however enhance heart survival, possibly by providing inorganic ions not present in the medium. By altering the sugars present and by addition of inorganic

phosphate Herold (1965) found that isolated *Helix* myocardia have a higher respiratory quotient in the presence of phosphate. Since the intensity of respiration did not alter much, he suggested that the $PO_4^{\equiv}$ was acting by increasing the rejection of CO_2, possibly through decarboxylation.

Some interesting experiments on organ culture with the marine prosobranch *Calyptraea sinensis* are reported by Streiff (1966, 1967a, b). In his earlier papers (1963, 1964) it is clearly brought out that different organs from the same animal survived better in different fluids. Streiff's media, modified from Wolff & Haffen (1952), all maintained organs for several weeks. However, he altered the concentrations of additives (e.g. cystein, albumin, beef embryo extract), and found that gonads do better on a rich medium, and the penis and tentacles do well on a medium with less organic additives. Sperm kept well in the seminal vesicles in several fluids, and the central nervous system contained neurosecretory substances after 83 days in culture. Digestive glands were kept for only 21 days, but were still alive at the end of the experiments.

Assessment of the viability of organs in culture may become a problem when the organ, such as a gonad, is capable of neither neurophysiological nor muscular activity. Thus, tentacles, hearts and other muscular organs have most often been used as survival indicators, and Benex (1967a, b, 1969) has recently used the densely ciliated gill filaments of *Mytilus* to assess the importance of certain chemical additives in her medium. This research has progressed to a very specific point where she has been selecting chemicals with related configurations and testing the importance of these. Her results show that the particular configuration of p-amino-benzoic acid, with a benzene nucleus and a free $-NH_2$ in the para position is all important. Her statement that possibly certain chemicals are important during cell divisions and others during 'normal' cell metabolism reflects the advanced state of her studies and the dynamic nature of the material being investigated.

In all experiments the quality of the organs begins to decrease after a time. In the early work of Zweibaum (1925), Bevelander & Martin (1949) and Sengel (1961), degeneration was quite marked after 5-7 days. When the tentacles of *Biomphalaria glabrata* survived for at least 4 weeks in a complex medium (Benex, 1966), the explant dedifferentiated to a spherical form with a center of mostly connective tissue. Benex (1966) has investigated the importance of nervous tissue in this process and found that in the absence of the eye plus its associated nerve mass, the tentacles were already spherical in 12 days, whereas together with these components the tentacles remained elongated for 12-15 days. Dedifferentiation, in this case at least, seems to be slowed by the presence of nervous tissue. It should be remembered that even in intact organisms, individual organs, with lack of use, can become dedifferentiated to a certain extent. On being removed from a body an organ may lose some of its functions and certainly loses any 'feedback' from those functions it retains; this feedback may be necessary to the proper maintenance of organ structure and physiology.

Since 1964 most molluscan organ culture work has been used to investigate the endocrinology of reproductive cycles. Durchon's paper (1963) and Sengel's longer paper (1964) drew attention to the possibilities in this field. The former author (Durchon & Richard, 1967) has investigated the role of the optic glands in ovarian development of the cuttlefish *Sepia officinalis* (L.). Freed from cerebral inhibition by removal from the parent body, the optic gland begins secretory activity. The secretion is hormonal, acting on the ovary to induce vitellogenesis in oocytes which are >0.3 mm diameter (this work parallels that of Wells & Wells (1959) who used an *in vivo* technique). In Durchon & Richard's

work, as in that of Benex (1964b), the tissues healed rapidly in culture. Within 4 days an epithelial envelope enrobed the explant. Such a phenomenon has also been reported by Choquet (1964). When optic glands and ovaries were grown in the same container, they often grew together within 8 days, the optic gland being overgrown by the ovary (Durchon & Richard, 1967). This happened even when the explants were from separate animals, indicating that incompatibility is not a problem in such circumstances. Even more surprising is that the young gonad of *Helix aspersa* and the nerve ring from adult *H. pomatia* will grow together within a few days *in vitro* (Guyard & Gomot, 1964).

Choquet (1964, 1965) and Streiff (1966, 1967a, b) have investigated reproductive endocrinology of marine prosobranchs. These authors and Guyard & Gomot (1964) have presented a great deal of valuable information on the hormonal control of reproduction in molluscs. Despite their interest, this is not the place to discuss those results; the methods of organ culture used are what presently concern us. All of them were modifications of a diphasic system, that is a solid gel overlain by a fluid medium. The components of the liquid phase varied, mostly with respect to the organic additives. Guyard & Gomot (1964) positively state that gonads of *Helix aspersa* will survive for a period in media without organic additives, but for differenciation of sex cells to take place, addition of *Helix* hemolymph, chick embryo extract, or nerve extract is essential. Embryo extract encouraged the female cells, stopping male cells at the spermatocyte stage. With snail hemolymph female cells were similarly encouraged and male cells developed to maturity. This 'normal' development takes place more rapidly *in vitro* than *in vivo*. The effect of nerve extracts here, as in other molluscs (Streiff, 1966), differs with the age of the donor, corresponding with changes in the neurosecretory cycles. Choquet (1965) reports that the temperature of the culture - 10 or 20° C - was unimportant to his results, and organs can be successfully cultured as fragments. Choquet was able to cut one gonad into several pieces and culture each with a separate organ from the same animal. Ganglia and tentacles were used, as has been done elsewhere (Guyard, 1967; Streiff, 1966, 1967a, b), as these organs have been shown to produce sex hormones in gastropods (Pelluet, 1964). It is important to realise, however, that *extracts* of endocrine organs may not reveal the presence of hormones, as these may be constantly released as they are produced at low concentrations. Better results are obtained when 2 or more organs are cultured together. Guyard (1967) has successfully cultured *Helix* ovotestis with cerebral ganglia from the prosobranch *Viviparus viviparus*, and by this means he demonstrated that hormones from female *Viviparus* markedly affect the sexuality of *Helix* gonad.

Streiff (1963, 1964, 1966, 1967a, b) also has chosen to work with a protandrous hermaphrodite, *Calyptraea sinensis*. The advantages of this are worth considering. As Sengel (1964) pointed out, organ culture permits 3 diverse activities to be investigated: (1) organ function, (2) organ growth, and (3) organ differenciation. It is advantageous therefore to use an animal which goes through, in its natural life history, one or more marked changes, particularly structural ones. The gradual attainment of maturity typical of most pulmonates does not provide ideal material. The situation found in insects, with their metamorphoses and moultings, is ideal. Perhaps the closest gastropod molluscs get to that situation is with the change of sex found in protandrous hermaphrodites. Other than that, possibly changes associated with aestivation and later resumption of activity may provide a useful area for investigation, but so far this has not been pursued. Certain bivalve molluscs exhibit sex changes (Galtsoff, 1961), but these have not been studied using organ culture techniques, although Lubet (1966) has discovered

clear-cut endocrine relationships in the reproductive process *in vivo*, using operative techniques on bivalves.

Streiff (1967a) claims that after 212 days in culture, organs remain in excellent condition. This, and the clear-cut changes taking place in the reproductive tract of *Calyptraea sinensis*, have permitted Streiff to go a long way towards full understanding of the hormonal control of reproduction in this animal. His findings have far-reaching implications. In particular he finds that there is a tendency for presumptive gametes to develop, in the absence of hormones, into oocytes. This 'autodifferenciation' may be a widespread phenomenon in gastropods, and needs to be drawn to the attention of other investigators. A complex system of interacting hormones, each active for different periods of time, has been suggested for *Calyptraea* (Streiff, 1967a).

One other line of investigation to which the phrase *in vitro* is applied is yielding useful information on organ and tissue physiology. This is the technique in which organs are homogenized and incubated with substrates (Friedl & Bayne, 1966). Results of this work, by providing more information on metabolic pathways and enzyme systems, will undoubtedly broaden the basis on which we must design culture media for whole organs.

CONCLUSIONS

1. Organ culture is a powerful tool for investigations of morphogenesis and endocrinology, and is readily applicable to molluscs. Specialized or expensive equipment is usually not necessary.
2. Each species and each organ requires its own conditions for optimal survival.
3. Whilst progress has been made on the provision of an adequate chemical environment for explants, little or no effort has been made to simulate *in vivo* physical conditions, such as pressure and blood circulation.

ABSTRACT

After reviewing the early development of *in vitro* studies, the paper discusses publications which have dealt with tissue culture of molluscs, since these have provided useful information for latter organ culture work. The methods used in these more recent organ culture studies are then reviewed. Mention is made of the more interesting physiological data to come from these investigations.

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Malacological Review, 1968, 1: 137-181

CONTENTS OF MALACOLOGICAL PERIODICALS, 1967

The current contents of major malacological periodicals, as shown by their tables of contents, are herewith reproduced, mostly with permission of their editors, as a service to our readers, especially to those that do not have access to larger libraries that subscribe to some or all of these publications. Some malacological publications that are published occasionally rather than periodically, have not been included in this issue, but their contents may be included in future numbers of *MALACOLOGICAL REVIEW*.

The publications listed here are all for the year 1967, except for the *Journal of the Malacological Society of Australia*, which did not have an issue for 1967. We are including No. 10 of that journal, which was published on 16 November 1966.

Publications for the year 1967, but which actually had publication dates in 1968, are included here. [For example, contents of *The American Malacological Union, Inc., Annual Reports for* 1967,, Bull. No. 34 (dated 1 December 1967, but listed as mailed to subscribers on 20 March 1968), are given on p 164-165].

Contents of *Comunicaciones de la Sociedad Malacológica del Uruguay* are included here for interest to readers, although this mimeographed issue may not actually constitute a "publication," as defined by the International Commission on Zoological Nomenclature [cf., Recommendation 8A, Article 8, Section III, *International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology*, pub. for Int. Comm. zool. Nomencl. by Int. Trust for Zool. Nomencl., London, 1961, 176 p (p 7)].

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[1]Year the journal was first published.

[2]Originally *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft*. Erster Jahrgang, 1869 (The first issue, No. 1 & 2, marked December, 1868). The last volume before the name was changed was for the year 1919 (Einundfünfzigster Jahrgang).

[3]Originally *The Quarterly Journal of Conchology* (Vol. 1, 1874).

[4]Originally *The Conchologists Exchange* (Vols. 1 & 2, 1886-1888).

[5](See bottom of next page).

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[5]Originally published as a list of officers and members together with the organization's constitution under the title *Members of the American Malacological Union* [dated 1 April 1932]; followed by *Mrs. Imogene C. Robertson's Rambling Notes on the Second Annual Meeting of the American Malacological Union in Washington, D. C., May 26-28, 1932,* 11 p [mimeographed]; *Report, Fourth Annual Meeting and Membership, The American Malacological Union* [dated 1 August 1934]; similar title for the fifth annual meeting [1935]; *The American Malacological Union* [1936-1941 (1942)]; *The American Malacological Union, News Bulletin and Annual Report* [1943-1951]; *The American Malacological Union, Annual Report* [1952-1954]; *The American Malacological Union, Annual Reports* [1955-1963]; *The American Malacological Union, Inc., Annual Reports* [1964-1968]. Thirty-five numbers have been published, including that for the year 1968 (Bull. No. 35). Since 1955 (Bull. No. 22), each year has had a consecutive "bulletin number."

[6]First issue for the year 1968.

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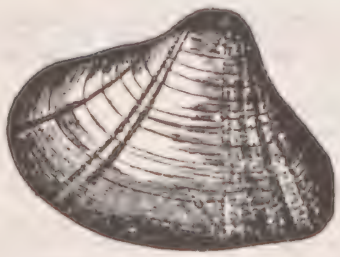

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Weitergeführt von Dr. W. WENZ und Dr. F. HAAS

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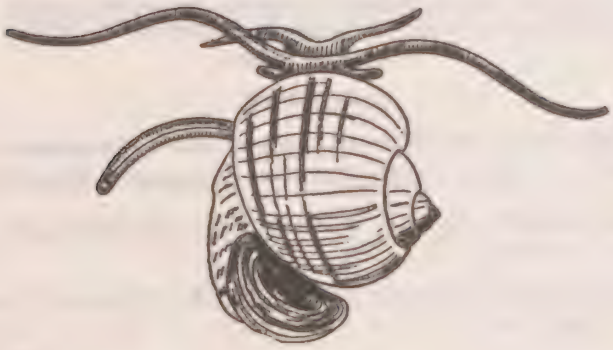

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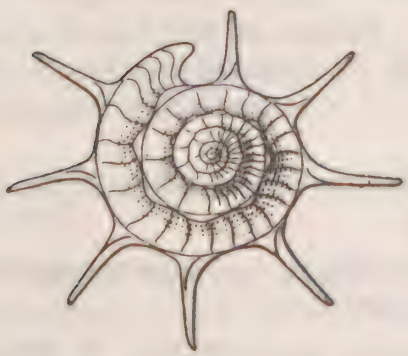

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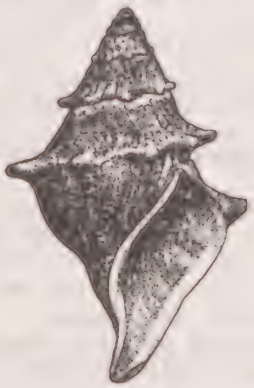

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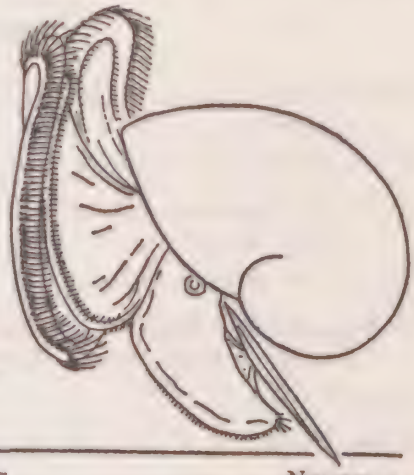

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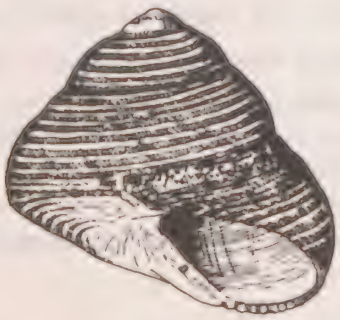

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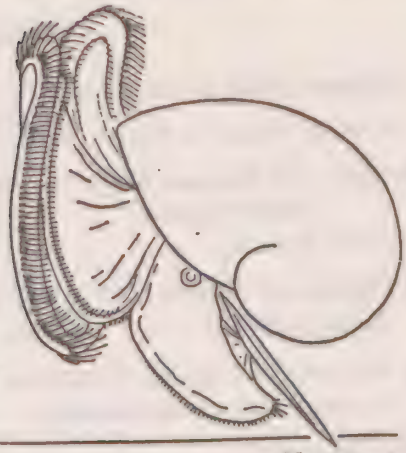

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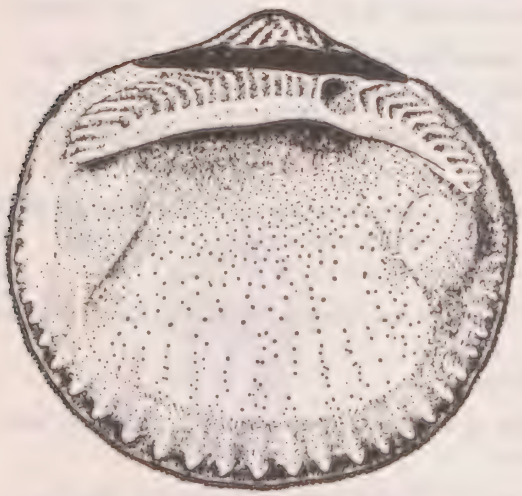

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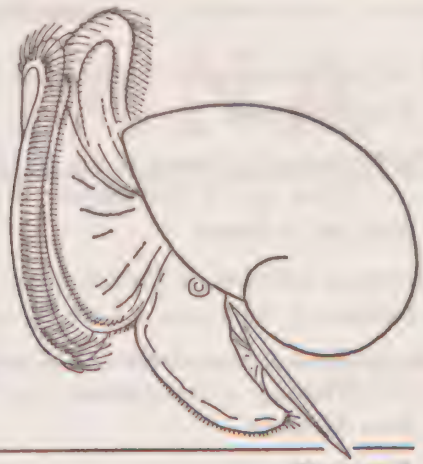

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